84- 2840 /

Canadian Special Publication of Fisheries and Aquatic Sciences 63

# Physiology and the Mariculture of some Northeastern Pacific Bivalve Molluscs

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DEPARTMENT OF FISHERIES AND OCEANS
*Ottawa 1983*

Published by

Government of Canada
Fisheries and Oceans

Scientific Information
and Publications Branch

Publié par

Gouvernement du Canada
Pêches et Océans

Direction de l'information
et des publications scientifiques

Ottawa K1A 0E6

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Available from authorized bookstore agents and
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Canadian Government Publishing Centre,
Supply and Services Canada, Hull, Que. K1A 0S9

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Canadian funds
to the Receiver General for Canada.

A deposit copy of this publication is also available
for reference in public libraries across Canada.

Canada: $4.00 Catalog No. Fs 41-31/63E
Other countries: $4.80 ISBN 0-660-11317-1
ISSN 0706-6481

Price subject to change without notice
Ottawa

Printed in Canada
by
Donald F. Runge Ltd.

Correct citation for this publication:

Bernard, F.R. 1983. Physiology and the mariculture of some
northeastern Pacific bivalve molluscs. Can. Spec. Publ. Fish.
Aquat. Sci. 63: 24 p.

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## Abstract

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Equations describing the effects of water temperature, salinity, oxygen, and food availability on ventilation and oxygen consumption rates of nine species of bivalve molluscs from the Oregonian Province are given. Experiments were conducted throughout the year to more closely approximate the natural cycle. Intrinsic physiological states, mediated by nutritional history, prevailing physical regimes and the gametic cycle, profoundly influence performance. Oxygen consumption and ventilation rates are proportional to body surface area, rather than weight, but rates are strongly influenced by body size and probably age.

Ventilation is determined by food needs rather than respiratory requirements. Development of long siphons, while affording protection in the deep infaunal habitat, lowers the ventilation efficiency, as estimated by oxygen uptake. Acclimatory ability to compensate for changing environmental conditions is not equally developed in bivalves and may be entirely absent in deepwater forms and strongly developed in high intertidal dwellers. There are important interactions between salinity and temperature on oxygen consumption in the Japanese oyster *(Crassostrea gigas)* and the butter clam *(Saxidomus giganteus)*. Oxygen tension appears to be a less important factor in the natural environment. The mussel *(Mytilus edulis)* and the Japanese oyster are most tolerant of wide variation in physical conditions and the weathervane scallop *(Patinopecten caurinus)* least so.



## Résumé

BERNARD, F. R. 1983. Physiology and the mariculture of some northeastern Pacific bivalve molluscs. Can. Spec. Publ. Fish. Aquat. Sci. 63: 24 p.

La présente publication contient des équations décrivant les effets de la température, de la salinité et de l'oxygène de l'eau et de la nourriture sur les taux de ventilation et de consommation d'oxygène chez neuf espèces de mollusques bivalves de la province Orégonienne. Afin de se rapprocher le plus possible du cycle naturel, nous avons mené des expériences tout au long de l'année. L'état physiologique intrinsèque, découlant de l'alimentation passée, les régimes physiques dominants et le cycle gamétique influent profondément sur la performance. Les taux de consommation d'oxygène et de ventilation sont proportionnels à la surface du corps plutôt qu'au poids, mais sont fortement influencés par la taille et probablement l'âge.

Nous avons déterminé la ventilation d'après les besoins alimentaires plutôt que les besoins respiratoires. Le développement de longs siphons, tout en fournissant une protection dans un habitat profond, diminue le rendement de la ventilation comme l'indique l'absorption d'oxygène. Tous les bivalves n'ont pas la même capacité d'acclimatation qui permet de compenser des conditions ambiantes changeantes. Cette capacité peut même manquer complètement chez les formes d'eaux profondes et être très développée chez les mollusques habitant dans la zone intertidale supérieure. Il y a interactions importantes entre la salinité et la température, d'une part, et la consommation d'oxygène, d'autre part, chez l'huître japonaise (*Crassostrea gigas*) et le clam de Washington (*Saxidomus giganteus*). La tension d'oxygène semble être un facteur moins important dans le milieu naturel. La moule (*Mytilus edulis*) et l'huître japonaise sont les espèces les plus tolérantes d'une forte variation des conditions physiques, tandis que le pétoncle d'Alaska (*Patinopecten caurinus*) est l'espèce la moins tolérante.

## INTRODUCTION

Bivalve molluscs were the first marine organisms cultivated and have long been recognized as representing the highest potential production of consumable protein per unit area of any type of cultivated organism. This is because in areas of adequate water exchange, bivalves concentrate the primary production of a wide region. Further, though feeding on minute particles, bivalves themselves are large enough to be directly utilized as food. This food chain with no intermediaries results in the direct conversion of primary production to harvestable protein.

For many years oysters were the only species cultivated and they have supported a significant industry on both the Atlantic and Pacific coasts of Canada. More recently attention has been given to the potential for use of other bivalve species. This interest is part of the general worldwide increase in mariculture, but it also has been stimulated by declining natural stocks of bivalves, due to overharvesting and loss of habitat, together with the obvious need to progressively replace gathering by managed production.

To date bivalve cultivation has usually been a matter of simply moving stock from poor to good growing areas, or by gathering juveniles and holding them in a suitable environment until growth to market size is completed. For the bivalves species traditionally cultivated the best regions for growth are estuarine and subject to conflicting demands and usage by other industries and urbanization. This has prompted attempts to raise bivalves in regions hitherto considered unsuitable, or to accelerate growth by manipulating one or more environmental factors. Species new to cultivation are also receiving attention and already have yielded spectacular results such as the scallop culture of northern Japan. In all cases progress beyond the most basic husbandry depends on an understanding of the environmental requirements of the mollusc.

This paper records the physiological behaviour and its modification by the environmental conditions characteristic of the seasonal climate of shallow water and intertidal zones where commercial species of clams are found. Though to the mariculturist the growth rate and mortality rate are the critical points of interest, it is not technically possible to directly measure these in the short term as they are obscured by competing seasonal factors of the life cycle. However, physiological activities such as oxygen consumption, or pumping rate are readily monitored, and furnish a good index of metabolic performance ultimately manifested in growth and survival. I thus present new data on respiration and pumping rates under different temperature, salinity, and oxygen supply regimes, and discuss their importance to production and survival. These data, combined with my observations during 20 yr of research and review of some of the more significant literature, are used to derive ranges and optima for environmental conditions most suitable for somatic growth for the nine species. The primary physiological literature is fragmented, conflicting, and difficult to approach and has been largely ignored by practical mariculturists. This is unfortunate, as it is precisely this basic information that is so important during feasibility studies, and it frequently suggests solutions to the practical problems encountered.

## BIVALVE FUNCTION

Most bivalves are completely enclosed within a box-like shell from which the mantle margins, sometimes prolonged into a long siphonal tube, and the foot can be protruded. However, the major interaction with the environment takes place via the ventilatory current. The gill is generally much enlarged and used to pump water in volumes greatly in excess of those required for respiration. The gill is also provided with ciliary and mucous systems for the interception and collection of suspended particles on which the clam feeds. The morphology of bivalves has been profoundly influenced by this dependence on pumping and removing nutritous particles from large quantities of water, and has allowed the group to colonize a wide range of aquatic habitats and undergo widespread radiation.

The passive lifestyle of bivalves, the external shell and dependence on the water pumped is reflected in the limited physical responses of bivalves to fluctuating external conditions, usually involving only the alteration of size and configuration of the openings through the gill, changes in rhythm and amplitude of the ciliary beat of the gill, and orientation and size of the pallial apertures. All these activities appear to be controlled by two mechanisms. The first is direct, instantaneous, and probably under neural control as severing the brachial nerve results in decreased or irregular ciliary activity (Paparo 1973). However, both mechano- and chemoreceptors are also involved, as bivalves may be shown to respond differentially to algae (Ballentine and Morton 1956). Typically this initial response results in considerable overreaction or "overshoot" in activity. The second component involves slow adaptive changes in activity, with long-term alterations of the basic metabolic pathways (Wieser 1973) tending always to bring performance rates towards medial levels of activity.

Actively moving organisms can avoid some of the environmental fluctuations typical of the intertidal and shallow water zones by seasonal or daily migrations. Bivalves are sedentary, often remaining in the same location their entire life or moving only a few centimetres. Some species such as scallops are able to move significant distances and may even undertake seasonal migrations. This means that most bivalves are obliged to tolerate prevailing conditions or cease activity. Like other cold-blooded animals, bivalves are sensitive to temperature and in the temperate regions where most bivalve mariculture occurs, this is the chief factor determining production. In these regions bivalves hibernate during the coldest weather, and growth is limited to a small fraction of the year. A further and very significant factor in shallow and estuarine waters is the frequent and rapid fluctuations in temperature and salinity due to movement of water masses and land drainage. Some protection from these stresses is afforded the deeply infaunal clams, but ventilation of the overlying water quickly obviates the insulating effect of the sediment and no physiological advantage is apparent.

Although temperature is the major environmental factor affecting performance, other factors such as salinity (Schlieper and Kowalski 1956), oxygen (Bayne 1971a), and concentration of suspended particles (Jorgensen 1966) all play interrelated roles. It is doubtful that in nature spatial distribution coincides entirely with the optima of these factors, but is also mediated by predation and niche availability. Though stressful conditions may be frequent, particularly in the intertidal region, changes in metabolic activities and rates cannot be directly interpreted as stress symptoms, but may be significant adaptations for the exploitation of transitory advantageous conditions.

Many bivalves have internal homeostatic mechanisms that maintain nearly uniform metabolic function rates in spite of external changes. However, this compensatory ability is limited, and too large or rapid a change results in stress or an imbalance between food uptake and energy expenditure, which may significantly affect performance rates and reduce survival. The external conditions permitting normal physiological function and an advantageous relationship between energy gain and loss is herein termed the *zone of function*. Survival outside the zone is possible, corresponding to the *zone of resistance* (Fry 1947) but performance is compromised, and too great a departure from the zone of function ultimately results in death.

Fry (1947) recognized three distinct levels of respiration in fish. The concept was applied to invertebrates by Halcrow and Boyd (1967) and extended later to the mussel *Mytilus edulis* (Thompson and Bayne 1972). These rates are summarized below; however, under natural conditions, one rarely predominates, and there is constant shifting towards a level consistent with the mutable prevailing conditions, matching ventilation (and therefore browsing rate) to food supply, or decreasing energy loss during periods of low temperature or starvation.

*Standard Metabolic Rate (SMR)* is the level of activity for the maintenance of vital functions of starved animals, or rate of fasting catabolism (Kleiber 1961). Ventilation and oxygen consumption are low and there may be reduced sensitivity to temperature. In oysters it has been termed *storage metabolism*.

*Routine Metabolic Rate (RMR)* is the level of metabolism of feeding animals and comprises the sum of the costs of ventilation, metabolism of ingested ration, and gonadal and somatic growth, as well as the basic vital functions (SMR). During times of exceptionally high concentration of suspended particles, appreciable energy may be lost to cleansing mucus production, and at other times locomotor activity may occur, but as these functions are ephemeral, the RMR is taken as the level of activity of a static subject dealing with optimal concentration of suspended particles.

*Active Metabolic Rate (AMR)* is the temporarily high level of activity stimulated by temperature increase or presence of food. The maximum AMR is elicited by a combination of warmer water and food, while the size of the response is dependent on whether it occurs during SMR or RMR.

## MATERIALS

The species investigated are members of the Oregonian Province of the northeastern Pacific extending from the Aleutian Archipelago to Central California. Closely related species occur at similar latitudes in the western Pacific and Atlantic oceans, but only the mussel *Mytilus edulis* is cosmopolitan. The clam *Tapes philippinarum* (Adams and Reeve 1850), formerly known as *Venerupis japonica* (Deshayes 1853), is well established in the region after accidental introduction with the cultivated Japanese oyster *Crassostrea gigas* (Thunberg 1795) which reproduces only sporadically on the Pacific coast of the United States and Canada (Quayle 1964).

The bivalves studied representing varied morphological types (Table 1) were collected from various habitats along the southeastern shores of Vancouver Island, British Columbia, Canada (49°N, 123°W). Scallops *(Patinopecten caurinus)* were trawled in late March and early April. Rock scallops *(Hinnites giganteus)* were obtained with SCUBA in April and July. The other species were sampled throughout the year and monitored close to ambient temperature, to represent the various physiological phases in the annual cycle. In all cases a size series was used to include small to large individuals but recently metamorphosed and extremely small individuals were not sampled. Additional specimens, such as gerontic individuals, were tested as necessary.

TABLE 1. List of species with vernacular name, distribution, and niche.

| Species | Name | Range | Depth | Niche |
|---|---|---|---|---|
| *Mytilus edulis* Linné, 1758 | Bay mussel | 27–74°N | Int. — 2 m | Epi. |
| *Hinnites giganteus* (Gray, 1825) | Rock scallop | 25–60°N | Int. — 3 m | Epi. |
| *Patinopecten caurinus* (Gould, 1850) | Weathervane scallop | 41–57°N | Int. — 150 m | Epi. |
| *Crassostrea gigas* (Thunberg, 1793) | Japanese oyster | 35–55°N | Int. | Epi. |
| *Clinocardium nuttallii* (Conrad, 1837) | Cockle | 33–60°N | Int. — 5 m | Inf. |
| *Tresus capax* (Gould, 1837) | Horse clam | 35–60°N | Int. — 15 m | Inf. |
| *Protothaca staminea* (Conrad, 1837) | Littleneck clam | 23–70°N | Int. — 3 m | Inf. |
| *Saxidomus giganteus* (Deshayes, 1839) | Butter clam | 45–60°N | Int. — 5 m | Inf. |
| *Tapes philippinarum* (Adams & Reeve, 1850) | Manila clam | 37–50°N | Int. | Inf. |

NOTE: Int. = intertidal; Epi. = epifaunal; Inf. = infaunal.

## METHODS

The temperature, salinity, and suspended particle relationships to ventilation and oxygen consumption were established using individuals of as uniform weight as possible to represent mature animals but still undergoing measurable somatic growth. The observations of *Tresus capax* are prejudiced towards small individuals as large animals could not be accommodated in the experimental apparatus. A correction for the effect of body weight was obtained from growth series from juvenile to large mature specimens.

Species that do not burrow were placed individually in glass petri dishes. Borrowing types were buried in washed gravel and coarse sand in battery jars or beakers. The containers were held near ambient temperature and salinity in circulating water. After 2 d, the temperature was adjusted $1°C \cdot d^{-1}$ until the experimental temperature was attained. A group of containers with their animals was removed and held in small aquaria for 30 d acclimation. One group was provided with temperature-adjusted seawater taken from the near surface of Departure Bay. The deepwater *P. caurinus* was held under similar conditions, but provided with water pumped from 30 m below the surface with no algal addition, to more closely approximate natural conditions. Another set of samples, held at identical temperature and salinity but with the water passed through a series of filters, terminating with a 2-μm candlewick, comprised the starved group. The declining functions correlated with increased somatic size were monitored using a growth series and were all done in May.

Sensitivity to salinity was determined using animals acclimated 20 d at 15°C and 30‰ in the fed condition. The salinity was then adjusted with distilled water or a concentrated Instant Ocean® solution. The salinity was changed in approximately 10‰ steps over 6 h and measured with an induction salinometer. Two hours of stabilization were allowed prior to activity measurements.

Ventilation and oxygen consumption were measured in an enclosed flow-through system (Fig. 1). Three chambers were used in parallel and the mean of the three taken as the rate. Observations were repeated at three intervals of 4 h to allow for changes in metabolic rates. Chamber perfusion was maintained at a minimum of 500 $mL \cdot min^{-1}$ to eliminate recirculation and proportionately increased at higher rates of ventilation, which constitutes a source of error for ventilation measurement. During phases of reduced metabolism, perfusion was reduced to 100 $mL \cdot min^{-1}$, but always maintained at a volume greater than ventilation. The "active" portion of the chamber was kept small by changing the volume of the section accommodating the experimental subject to fit its size. Inflow and outflow ports were carefully levelled to prevent any hydrostatic imbalance.

Ventilation was determined two ways. A Model B Coulter Electronic Particle Counter® monitored the difference between particle populations in the outflow using the method of Sheldon and Parsons (1967), multiplied by the chamber perfusion rate. The rapidity of the electronic particle counter permitted sampling at various chamber flow rates, and the volume when no further increase in particle retention was observed was taken as the filtration rate using the method described by Möhlenberg and Riisgård (1979). Experiments showed that the unicellular alga *Tetraselmis* and plastic spherules >15 μm were entirely retained, so filtration rate was considered equivalent to total ventilation. Chamber flow rates were maintained well above the maximum ventilation rate, obviating the errors introduced by internal recirculation in flow-through systems (Riisgård 1977). The small chamber volume, coupled with gentle stirring, eliminated "dead" spaces reducing errors in true particle concentration of the inhalant stream (Hildreth and Crisp 1976) to insignificance. Calculations were based on several size categories and periodically tested with 15-μm plastic spherules (Dow Chemical). Particles >2 μm were used to eliminate errors due to production of small particles by the bivalve (Hildreth 1980) that could result in underestimate of uptake. Ventilation was also monitored by heat loss from a heated thermister probe placed in the exhalant stream (McCammon 1965). This system detected the extremely low levels of ventilation during starvation at low temperature and was left in place during indirect (particle retention) estimates of ventilation. Oxygen consumption was

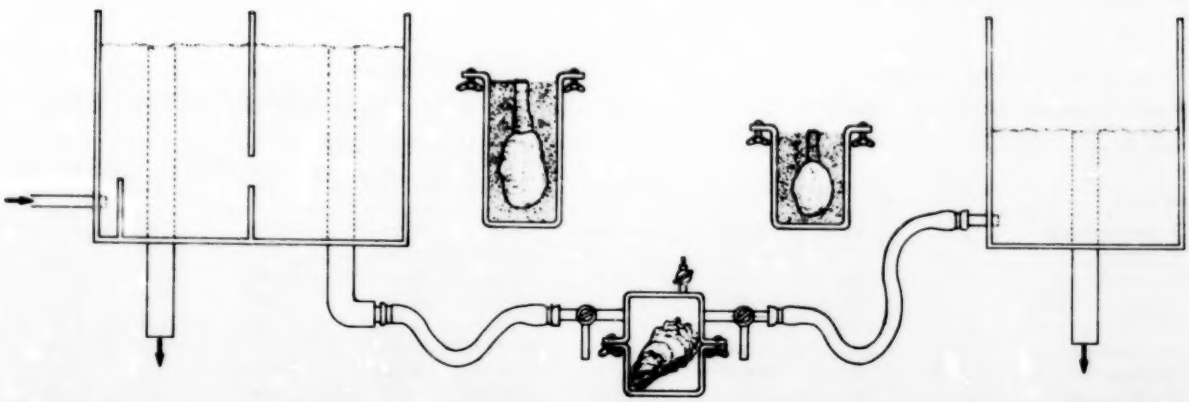

FIG. 1. Continuous flow apparatus used to measure ventilation and oxygen consumption of bivalves. The specimen container is changeable to ensure minimum chamber volume.

monitored using a portion of the sample removed for particle counts, using the standard Winkler titration, modified for small samples (Strickland and Parsons 1968).

Two series of experiments were conducted covering the accelerated ventilation and oxygen consumption due to increased temperature and suspended food. The first series used animals acclimated to 30 d at 10°C and 30‰ in the fed and starved state. The temperature was then raised 2°C·d$^{-1}$ and performance monitored. The second series used individuals after the metabolic rate determinations.

The dry body weight of a subsample was obtained before each experiment to establish whether there was any change. At termination all bivalves were opened and the flesh was removed and weighed after drying to constant weight at 100°C. The dry meat weights were used to present weight-specific observations. The relationship of external factors to ventilation and oxygen consumption was calculated by regression equations using the least squares method.

The size-frequency of particles retained was obtained from the Coulter Counter during the routine ventilation rate determinations, and a second series of bivalves acclimated at 14°C and 30‰ was used to determine whether particle size selectivity existed. Natural plankton was used, obtained by net from Departure Bay. Missing sizes in the size-range spectrum were provided by addition of cultured *Monochrysis* (3–5 μm diam) or *Tetraselmis* (5–10 μm diam). Observation showed commonly used inorganic particles to be inhibitory to ventilation, but not uptake. Kieselguhr, bentonite and Fuller's earth all depressed performance, but "natural" suspensions comprising chiefly clay and dry particles showed no inhibitory effect. Counts were made at various equivalent spherical sizes and selectivity was tested using the Jacobs (1974) Electivity Index modified from Ivlev (1961). Total weights of suspended particulate materials were calculated using preweighed glass filters and the organic portion determined by wet oxidation (Strickland and Parsons 1968).

## RESULTS

The raw observations (Bernard 1983) were pooled and subjected to standard statistical treatment. Relationships between oxygen consumption, ventilation, and size, are conveniently expressed by an allometric curve fit (Table 2). The exponents are all positive, ranging between 0.35–0.70 for ventilation and 0.65–0.84 for oxygen consumption, conforming generally to the values calculated in Bayne (1976) except for very large *Mytilus californianus* which yielded negative exponents. The exponents for ventilation are smaller than those for oxygen uptake indicating either an advantageous relationship between efficiency and size or increasing sensitivity to possibly inimical laboratory conditions. Comparative interspecific observations may be expressed as rate per unit body weight to yield the $QO_2$ (mL $O_2 \cdot h^{-1} \cdot g^{-1}$) for oxygen consumption and similarly the $QV_2$ ($L \cdot h^{-1} \cdot g^{-1}$) for ventilation. Reference may also be made to a dimensionless standard body weight obtained by dividing with $W^b$ to give the $SO_2$ and $SV_2$.

Because of marked shifts of the metabolic optima and end points due to seasonal variations in temperature, activities were monitored on subjects collected at various times during the year to more closely approximate the true annual cycle, with determinations of RMR and AMR made at approximately normal concentrations of suspended food particles. The results represent the limits of thermal tolerance and the zones of normal ventilation and oxygen consumption. Low temperature results in closure of the shell valves with little or no measurable metabolic activity, though the pallial openings may be fully expanded. Increased temperature results in slight and unstable activity until the *lower thermal threshold* is passed, when a large and abrupt increase in activity occurs. Then follows the *zone of function*, which is the thermal range where ventilation and oxygen consumption are regular and vigorous. A temperature is attained where activity becomes irregular, the adductor muscles relax, the mantle margins are become insensitive to tactile stimulus' and ventilation ceases. This point is here termed the *upper thermal threshold*.

The responses of ventilation and oxygen consumption to change of temperature were monitored over the zone of function of starved and actively feeding individuals. Starved animals, operating in SMR, increased oxygen comsumption and ventilation rates as temperature increased. This linear correlation is presented in Table 3, ordered by decreasing

TABLE 2. Regression constants of ventilation (L·h$^{-1}$) and oxygen consumption (mL $O_2 \cdot h^{-1}$) on dry weight flesh (g) in nine species of Bivalvia acclimated at 15°C, salinity 29‰.

| | | | Ventilation | | | Oxygen consumption | | |
|---|---|---|---|---|---|---|---|---|
| Species | *n* | Wt. range | *a* | *b* | $r^2$ | *a* | *b* | $r^2$ |
| *T. philippinarum* | 12 | 0.33–2.76 | 3.706 | 0.698 | 0.91 | 0.518 | 0.807 | 0.90 |
| *C. nuttallii* | 18 | 0.68–6.68 | 3.770 | 0.607 | 0.92 | 0.733 | 0.778 | 0.77 |
| *M. edulis* | 22 | 0.18–1.67 | 1.166 | 0.565 | 0.90 | 0.340 | 0.787 | 0.95 |
| *C. gigas* | 26 | 0.51–6.50 | 5.132 | 0.556 | 0.94 | 0.708 | 0.737 | 0.86 |
| *P. caurinus* | 10 | 2.31–7.88 | 2.121 | 0.553 | 0.80 | 0.920 | 0.836 | 0.81 |
| *P. staminea* | 25 | 0.44–3.86 | 2.171 | 0.517 | 0.84 | 1.477 | 0.829 | 0.88 |
| *H. giganteus* | 5 | 4.32–8.60 | 1.366 | 0.474 | 0.94 | 0.842 | 0.652 | 0.80 |
| *S. giganteus* | 23 | 0.30–7.07 | 1.281 | 0.430 | 0.91 | 0.924 | 0.655 | 0.90 |
| *T. capax* | 12 | 4.83–16.81 | 1.652 | 0.354 | 0.96 | 9.909 | 0.667 | 0.56 |

NOTE: *a* and *b* are fitted parameters in the power curve equation $Y = aX^b$; $X$ = body dry weight; $r^2$ = correlation coefficient.

slope values (b) as a biologically significant indicator of thermal dependence. Fed animals, in RMR, were more independent and severed a relationship which may be expressed as a logarithmic curve, except for the scallop *P. caurinus* where the best fit remains linear (Table 4). The downward displacement of the upper end of the R/T curve of the other species is attributable to decreased thermal sensitivity resulting from acclimatory processes.

The response during AMR varies whether the original state is SMR (starved) or RMR (fed). In the former case the response to a 5°C increase over the acclimated temperature is linear for ventilation (Table 5), representing a simple upward shift of the regression line, but a power function for oxygen consumption. For animals responding from RMR, the AMR curve is best expressed by a power function for ventilation, but linear for oxygen consumption, again, except for *P. caurinus* where it remains linear (Table 6). These linear and nonlinear models are significantly different, their biological significance being the capacity to partly increase oxygen comsumption from its depressed uptake during SMR. On the other hand, ventilation rates are most temperature dependent during RMR.

Maximum acute rates of oxygen consumption and ventilation occur with changes of 5°C or less. For animals

TABLE 3. Regression constants of ventilation ($L \cdot h^{-1}$) and oxygen consumption (mL $O_2 \cdot h^{-1}$) on acclimation temperature (°C) in nine species of Bivalvia during Standard Metabolic Rate, salinity 29‰.

| Species | *n* | Wt. (g) | Range °C | Ventilation | | | Oxygen consumption | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | *a* | *b* | $r^2$ | *a* | *b* | $r^2$ |
| *P. caurinus* | 36 | 7.21 | 4–15 | 0.671 | 0.123 | 0.81 | 0.110 | 0.007 | 0.69 |
| *S. giganteus* | 36 | 2.98 | 5–21 | –0.297 | 0.086 | 0.82 | 0.079 | 0.029 | 0.76 |
| *T. philippinarum* | 45 | 0.59 | 5–25 | –0.289 | 0.080 | 0.92 | 0.117 | 0.017 | 0.76 |
| *T. capax* | 36 | 7.08 | 6–20 | 0.078 | 0.072 | 0.84 | 0.573 | 0.010 | 0.64 |
| *H. giganteus* | 36 | 7.63 | 5–20 | 0.063 | 0.063 | 0.78 | 0.149 | 0.003 | 0.67 |
| *P. staminea* | 36 | 0.71 | 6–20 | –0.260 | 0.062 | 0.88 | 0.070 | 0.010 | 0.70 |
| *C. nuttallii* | 36 | 3.29 | 4–22 | 0.105 | 0.046 | 0.70 | 0.188 | 0.009 | 0.78 |
| *C. gigas* | 54 | 1.43 | 4–28 | 0.087 | 0.044 | 0.85 | –0.006 | 0.008 | 0.89 |
| *M. edulis* | 60 | 0.27 | 2–25 | –0.010 | 0.043 | 0.91 | 0.050 | 0.005 | 0.75 |

NOTE: *a* and *b* are fitted parameters in the linear equation $Y = a + bX$, where $X$ = temperature, $r^2$ = correlation coefficient.

TABLE 4. Regression constants of ventilation ($L \cdot h^{-1}$) and oxygen consumption (mL $O_2 \cdot h^{-1}$) on acclimation temperature in nine species of Bivalvia during Routine Metabolic Rate, salinity 29-30‰.

| Species | *n* | Wt. (g) | Range °C | Ventilation | | | Oxygen consumption | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | *a* | *b* | $r^2$ | *a* | b | $r^2$ |
| *T. capax* | 36 | 7.21 | 6–20 | –2.196 | 1.899 | 0.87 | 0.283 | 0.226 | 0.84 |
| *P. caurinus* | 36 | 6.83 | 4–15 | 0.575 | 1.757 | 0.79[1] | –0.047 | 0.200 | 0.78[2] |
| *H. giganteus* | 35 | 7.33 | 5–20 | –0.663 | 1.662 | 0.86 | –0.022 | 0.141 | 0.84 |
| *P. staminea* | 36 | 0.62 | 6–20 | –1.423 | 1.561 | 0.89 | –1.005 | 0.844 | 0.85 |
| *S. giganteus* | 40 | 3.05 | 5–21 | –1.455 | 1.382 | 0.90 | –0.473 | 0.473 | 0.96 |
| *C. nuttallii* | 36 | 3.92 | 4–22 | –0.634 | 1.244 | 0.72 | 0.085 | 0.160 | 0.88 |
| *T. philippinarum* | 45 | 0.69 | 5–25 | –0.189 | 1.208 | 0.81 | 0.149 | 0.131 | 0.85 |
| *C. gigas* | 54 | 1.67 | 4–28 | 0.553 | 1.112 | 0.73 | 0.053 | 0.136 | 0.89 |
| *M. edulis* | 60 | 0.32 | 2–25 | –0.232 | 0.923 | 0.91 | 0.061 | 0.140 | 0.92 |

NOTE: *a* and *b* are fitted parameters in the logarithmic curve equation $Y = a + b\ln X$, where $X$ = temperature, $r^2$ = correlation coefficient. [1]Linear equation = 1.469 + 0.290; $r^2$ = 0.90. [2]Linear equation = 0.054 + 0.033$X$; $r^2$ = 0.89.

TABLE 5. Regression constants of ventilation ($L \cdot h^{-1}$) and oxygen consumption (mL $O_2 \cdot h^{-1}$) on temperature (°C) in nine species of Bivalvia during Acute Metabolic Rate from Standard Metabolic Rate after 5°C increase, salinity 29‰.

| Species | *n* | Wt. (g) | Range °C | Ventilation[1] | | | Oxygen consumption[2] | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | *a* | *b* | $r^2$ | *a* | *b* | $r^2$ |
| *P. caurinus* | 28 | 7.63 | 9–15 | 1.521 | 0.208 | 0.82 | 0.072 | 0.625 | 0.76 |
| *S. giganteus* | 31 | 2.81 | 10–25 | –0.447 | 0.133 | 0.94 | 0.204 | 0.455 | 0.70 |
| *T. capax* | 30 | 7.24 | 11–25 | 0.648 | 0.130 | 0.72 | 0.472 | 0.262 | 0.77 |
| *P. staminea* | 29 | 0.82 | 11–25 | 0.259 | 0.110 | 0.86 | 0.112 | 0.448 | 0.94 |
| *H. giganteus* | 35 | 7.20 | 10–25 | 0.562 | 0.060 | 0.78 | 0.095 | 0.375 | 0.75 |
| *T. philippinarum* | 42 | 0.61 | 10–25 | 0.515 | 0.056 | 0.70 | 0.242 | 0.227 | 0.76 |
| *C. nuttallii* | 35 | 3.28 | 9–25 | 0.218 | 0.050 | 0.90 | 0.104 | 0.427 | 0.81 |
| *M. edulis* | 50 | 0.33 | 7–25 | 0.195 | 0.047 | 0.73 | 0.048 | 0.613 | 0.83 |
| *C. gigas* | 51 | 1.31 | 9–25 | 0.592 | 0.026 | 0.79 | 0.144 | 0.216 | 0.79 |

NOTE: *a* and *b* are fitted parameters in (1) ventilation linear equation $Y = a + bX$; (2) oxygen consumption, power curve $Y = aX^b$; when $X$ = temperature, $r^2$ = correlation coefficient.

acclimated to 15°C and then subjected to increased temperature at the rate of 0.2°C per min, the instantaneous R/T curve within the zone of function is bell-shaped with a maximum at 20°C. This relationship is best described with a second degree polynomial equation, and the values for oxygen consumption are given in Table 7. The acclimatory temperature shifts the point of maximum thermal sensitivity and the overall rate of function.

Increasing salinity from 30‰ to higher than local marine values (32‰) has little effect, but increases >10% result in decreased activity. Decreasing salinity is stressful as estimated by oxygen consumption and ventilation rates. Animals of different body size did not differ significantly in sensitivity. No difference was found in the reaction of starved (SMR) or fed (RMR) animals, and as oxygen consumption and ventilatory ratios remained stable, results are discussed in terms of ventilation only.

The low salinity value that results in signs of stress or valve closure is here termed the *critical salinity* and describes the lower limit of the *salinity zone of function*. The total response curve is bell-shaped due to increasing sensitivity as salinity departs further from the acclimated value. The regressions for the nine species examined showed similar slopes when subjected to 10% stepped salinity changes. When expressed as a percentage of the original rate the decrease is linear ($Y = -54.2 + 5.9$) between 30‰ and the individual critical salinities for the species. The 72-hr LD50 and the instantaneous critical declining salinities are given in Table 8. Time for recovery from changes in salinity increases as the changes get larger. Acclimation time for salinity changes, arbitrarily calculated as the number of days required for the bivalve to recover 80% of the original ventilation rate, varied widely for the various species (Table 9).

Van Winkle and Mangum (1975) examined various regression models for the analysis of oxygen uptake against ambient oxygen tension and concluded that the quadratic polynomial model provided the best statistical fit while permitting interspecific comparisons. As most of the literature

TABLE 6. Regression constants of ventilation ($L \cdot h^{-1}$) and oxygen consumption (mL $O_2 \cdot h^{-1}$) on temperature (°C) in nine species of Bivalvia during Acute from Routine Metabolic Rate 5°C increase, salinity 29‰.

| Species | *n* | Wt. (g) | Range °C | Ventilation[1] *a* | *b* | $r^2$ | Oxygen consumption[2] *a* | *b* | $r^2$ |
|---|---|---|---|---|---|---|---|---|---|
| *H. giganteus* | 33 | 7.11 | 10–25 | 0.675 | 0.693 | 0.81 | 0.171 | 0.021 | 0.92 |
| *P. staminea* | 30 | 0.75 | 11–25 | 0.818 | 0.611 | 0.91 | 0.251 | 0.067 | 0.86 |
| *S. giganteus* | 36 | 7.50 | 10–25 | 0.824 | 0.551 | 0.80 | 0.490 | 0.052 | 0.70 |
| *C. nuttallii* | 36 | 3.92 | 9–25 | 0.856 | 0.537 | 0.88 | 0.341 | 0.019 | 0.91 |
| *T. capax* | 30 | 6.83 | 9–25 | 1.303 | 0.514 | 0.95 | 0.427 | 0.105 | 0.92 |
| *M. edulis* | 52 | 0.41 | 7–25 | 1.208 | 0.468 | 0.81 | 0.278 | 0.060 | 0.88 |
| *P. caurinus* | 28 | 7.14 | 9–15 | 2.058 | 0.457 | 0.87[3] | 0.211 | 0.043 | 0.83 |
| *C. gigas* | 54 | 1.67 | 9–25 | 2.243 | 0.339 | 0.83 | 0.414 | 0.038 | 0.84 |
| *T. philippinarum* | 42 | 0.66 | 10–25 | 1.770 | 0.330 | 0.70 | 0.285 | 0.041 | 0.71 |

NOTE *a* and *b* are fitted parameters in (1) ventilation power curve $Y = aX^b$; (2) oxygen consumption, linear equation $Y = a + bX$, where $X$ = temperature, $r^2$ = correlation coefficient. (3) Linear equation = $2.713 + 0.307X$; $r^2 = 0.92$.

TABLE 7. Regression constants of oxygen consumption (mL $O_2 \cdot h^{-1}$) on temperature in nine species of Bivalvia during instantaneous acute from Routine Metabolic Rate after acclimation to 15°C, salinity 30‰.

| Species | *n* | Range °C | $B_0$ | $B_1$ | $B_2$ | $r^2$ |
|---|---|---|---|---|---|---|
| *M. edulis* | 30 | 2–25 | –0.697 | 0.153 | –0.0042 | 0.87 |
| *P. caurinus* | 6 | 2–15 | –0.606 | 0.161 | –0.0045 | 0.83 |
| *T. capax* | 10 | 5–20 | –0.637 | 0.126 | –0.0034 | 0.79 |
| *P. staminea* | 15 | 5–25 | –0.677 | 0.169 | –0.0049 | 0.95 |
| *S. giganteus* | 8 | 5–20 | –0.990 | 0.230 | –0.0065 | 0.84 |
| *C. nuttallii* | 12 | 5–20 | –0.671 | 0.142 | –0.0039 | 0.87 |
| *T. philippinarum* | 25 | 5–25 | –0.581 | 0.153 | –0.0044 | 0.76 |
| *H. giganteus* | 7 | 5–20 | –0.325 | 0.083 | –0.0022 | 0.83 |
| *C. gigas* | 29 | 5–25 | –0.680 | 0.141 | –0.0034 | 0.75 |

NOTE: The parameters are fitted functions of the second degree polynomial equation $Y = B_0 + B_1X + B_2X^2$, where $X$ = temperature, $r^2$ = correlation coefficient.

TABLE 8. Critical salinity for ventilation with 72-hr LD 50% for nine species of Bivalvia acclimated at 30‰ 10°C.

| Species | LD 50% | % | Species | LD 50% | % | Species | LD 50% | % |
|---|---|---|---|---|---|---|---|---|
| *P. caurinus* | 22 | ≈24 | *C. nuttallii* | 12 | 21 | *T. philippinarum* | 8 | 15 |
| *H. giganteus* | 19 | 22 | *T. capax* | 15 | 20 | *C. gigas* | 8 | 12 |
| *S. giganteus* | 15 | 21 | *P. staminea* | 10 | 20 | *M. edulis* | 5 | 9 |

TABLE 9. Mean calculated days to ventilatory recovery[a] for nine species of Bivalvia subjected to decreased salinity after acclimation at 20‰ and 12°C.

| Species | 27‰ | 24‰ | 21‰ | 18‰ | 15‰ | 12‰ |
|---|---|---|---|---|---|---|
| *P. caurinus* | 61 | | | | | |
| *H. giganteus* | 50 | >70 | | | | |
| *T. capax* | 54 | >70 | >70 | | | |
| *S. giganteus* | 60 | >70 | >70 | | | |
| *P. staminea* | 32 | 60 | >70 | >70 | | |
| *C. nuttallii* | 35 | 47 | 67 | >70 | | |
| *T. philippinarum* | 15 | 21 | 48 | >70 | | |
| *C. gigas* | 30 | 44 | 59 | >60 | >62 | >70 |
| *M. edulis* | 20 | 37 | 63 | >70 | >70 | >70 |

[a]Arbitrarily set at 80% of the original ventilation rate.

TABLE 10. Regression constants of oxygen consumption (mL $O_2 \cdot h^{-1}$) on ambient oxygen (mm Hg) in nine species of Bivalvia during standard (SMR) and Routine (RMR) Metabolic Rates. 29‰, 12°C.

| | SMR | | | | RMR | | | |
|---|---|---|---|---|---|---|---|---|
| Species | $B_0$ | $B_1$ | $B_2$ | $r^2$ | $B_0$ | $B_1$ | $B_2$ | $X^2$ |
| *M. edulis* | –0.014 | $7.2 \times 10^{-3}$ | | 0.97 | 0.170 | $17.3 \times 10^{-3}$ | $-6 \times 10^{-5}$ | 0.93 |
| *P. caurinus* | 0.026 | $18 \times 10^{-3}$ | $-9 \times 10^{-5}$ | 0.91 | 0.029 | $18.4 \times 10^{-3}$ | $-10 \times 10^{-5}$ | 0.91 |
| *S. giganteus* | 0.013 | $12.2 \times 10^{-3}$ | $-3 \times 10^{-5}$ | 0.95 | –0.103 | $18.3 \times 10^{-3}$ | $-7 \times 10^{-5}$ | 0.88 |
| *T. philippinarum* | 0.401 | $19.4 \times 10^{-3}$ | $-6 \times 10^{-5}$ | 0.91 | –0.560 | $27.6 \times 10^{-3}$ | $-12 \times 10^{-5}$ | 0.87 |
| *T. capax* | –0.131 | $14.7 \times 10^{-3}$ | $-4 \times 10^{-5}$ | 0.89 | –0.063 | $21.1 \times 10^{-3}$ | $-10 \times 10^{-5}$ | 0.86 |
| *H. giganteus* | –0.101 | $14.3 \times 10^{-3}$ | $-4 \times 10^{-5}$ | 0.82 | 0.095 | $17.6 \times 10^{-3}$ | $-8 \times 10^{-5}$ | 0.87 |
| *P. staminea* | –0.073 | $8.8 \times 10^{-3}$ | $-1 \times 10^{-5}$ | 0.80 | –0.150 | $22.2 \times 10^{-3}$ | $-11 \times 10^{-5}$ | 0.89 |
| *C. nuttallii* | 0.224 | $2.0 \times 10^{-3}$ | 0 | 0.84 | –0.250 | $20.4 \times 10^{-3}$ | $-9 \times 10^{-5}$ | 0.81 |
| *C. gigas* | –0.041 | $8.0 \times 10^{-3}$ | 0 | 0.85 | 0.088 | $20.2 \times 10^{-3}$ | $-8 \times 10^{-5}$ | 0.78 |

NOTE: $B_0$, $B_1$ and $B_2$ are fitted parameters in the second degree polynomial equation $Y = B_0 + B_1X + B_2X^2$ where $X$ = partial pressure oxygen, $r^2$ = correlation coefficient.

represents dissolved oxygen as a partial pressure of gas, conversion factors (Pierce et al. 1973) were used to transform mm Hg to mL $O_2$/L. The calculated function for the second degree polynomial equation describing oxygen consumption during SMR and RMR in relation to ambient oxygen reveal significant differences (Table 10).

Differential effects are pronounced for various combinations of temperature and salinity on the ventilation rates of *C. gigas* and *S. giganteus*. There is greater sensitivity to reduced salinity with increasing temperature for species inhabiting the mid-tidal zone, so the infaunal *S. giganteus* is more sensitive than the high intertidal epifaunal *C. gigas*.

## DISCUSSION

Experimental design and the handling of bivalves are critical when establishing metabolic rates determined by oxygen consumption or pumping rates, as these factors are sensitive to numerous external and internal conditions. It is probable that these two factors alone are responsible for a large portion of the differences in published estimates of bivalve physiology. Further difficulties derive from individual variations. Though directly responding to external factors, bivalves are not automata and some individuals of one species may undergo periods of negligible activity, or the shell valves may remain closed during apparently ideal conditions and periods of intermittent function occur (Newell 1966). Further, some individuals display consistently higher or lower metabolic rates than the general population. This variability may be genotypic (Haley et al. 1975) and account for individual growth disparities in populations maintained under identical conditions. Timing of the observations may also influence performance. It has been suggested that for some bivalves a persistent lunar cycle in shell opening occurs (Brown 1954; Brown et al. 1956), but reinterpretation of the data did not support this interpretation (Enright 1965). No cyclic pattern could be discerned in the species used in the present study, the shell valves remaining open most of the time during suitable external conditions as noted for oysters by Loosanoff and Nomejko (1946). This is to be expected as closure of the valves requires constant contraction of the adductor muscles working against the ligament. It is well known that bivalve function may be intermittent (Newell 1966), with wide, possibly cyclic patterns in performance (De Wilde 1973). Tidal rhythms of valve opening are well established (Morton 1970). Observations on several subtidal species failed to reveal any cyclic pattern, but pronounced individual variations were present. Rates of ventilation and oxygen consumption are temperature dependent, but amount of time the shell valves remain open is also temperature correlated and varies between 5–95% at and 30°C, respectively, for the oyster *C. gigas* (Bernard 1972).

Besides these intrinsic variations of response described above, attempts to determine the effects of the physical parameters acting upon a complex ecological system by

examining a single factor in isolation is not representative of the natural condition. However, it is only by such dissection of component factors that an understanding of the total picture may be built up. For this study I held bivalves in a uniform environment until a steady-state functional pattern was established; then the immediate effect of a change in a physical factor was noted and followed until the eventual establishment of a new steady-stage. The extrapolation of these findings to the natural situation must be circumspect, as uniform conditions are rarely met in nature. In fact, the shallow water and estuarine environment is characterized by frequent and abrupt fluctuations of nearly all the physical conditions. In order to more closely approximate these natural responses, bivalves were collected throughout the year and tested at close to ambient temperature to determine the annual activity cycle, and determine changes due to acclimation.

The ventilation and oxygen consumption rates observed by me are generally significantly lower than those reported in much of the literature. I argue that my results based on the mean performance of three individuals over a 12-h period made several times a year, more closely approximates the natural state and may be used for extrapolation for the estimation of seasonal function. The prolonged acclimatory times and special care given not to stress the bivalves may also contribute to my lower estimates. Even with the standardized treatment of all experiments, considerable variability occurred, but dormant or sluggish individuals were not excluded. Observations made on *C. gigas*, together with the estimates of individual variations (Fig. 2) are representative of the entire series. While it is probable that my experimental design is responsible for the lower metabolic rates recorded there is some evidence that the intrinsic physiological rates of local bivalves may be lower than those from other regions. This appears to be true for the supposedly cosmopolitan mussel *M. edulis* which appears to grow faster in the Atlantic than off British Columbia (Fig. 3). The very fast rates of growth in Spain are attributable to the elevated thermal minimum (Fig. 3d), but under conditions nearly similar to British Columbia in Scotland (Fig. 3c) growth was faster, and also in the apparently less ideal conditions in Nova Scotia (Fig. 3b). These differences appear to be general, so are not likely to be the result of microhabitat. Growth may be accepted as a general index of metabolic rate, so some genetic change in physiological capacity may have occurred in a species where the Pacific and Atlantic populations have been separate since the Early Pliocene.

Changes in external conditions result in alteration of metabolic rates. The response of an organism is primarily dependent on three characteristics of the parameter under consideration: its mean value, variance, and temporal pattern. The mean value sets the broad limits to survival, and hence, distribution. The variance challenges the intrinsic adaptability of the species. The temporal pattern determines the response route and rate. This includes the critical seasonality factor, as response is largely controlled by the internal physiological conditions, particularly the gametogenic cycle. In the case of gradual change, in-step physiological adaptation may occur, while more abrupt or extensive change will result in a disturbed performance that may be adjusted over time by an acclimatory mechanism, if present. Abrupt short-term changes may be avoided by suspending activity, but ultimately stationary organisms such as bivalves must physiologically adapt to environmental conditions. The permutations of these three criteria involving external factors, together with genetically determined potentials and the strong influence exerted by current physiological state, result in a wide array of responses to similar conditions.

Published estimates of bivalve metabolic rates are frequently based on oxygen consumption, although it may be more significant to use ventilation. Oxygen consumption is the product of many activities, including somatic and gonadal production, shell deposition, accumulation or mobiliza-

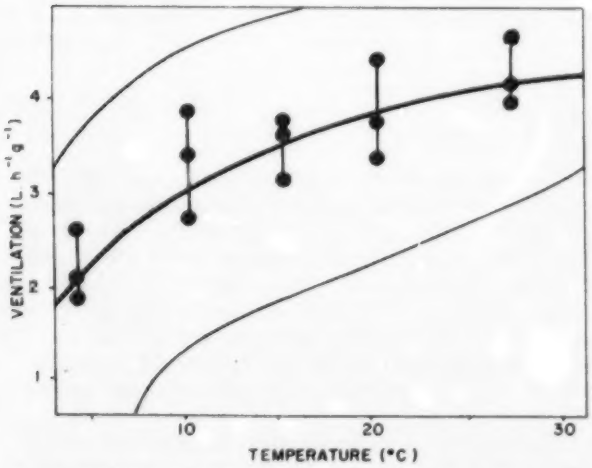


FIG. 2. Routine rates of ventilation as a function of temperature in the oyster *C. gigas*. Points represent means of three individuals taken at 4-h intervals. Stippled area shows 90% probability of individual variation. Calculated regression line.

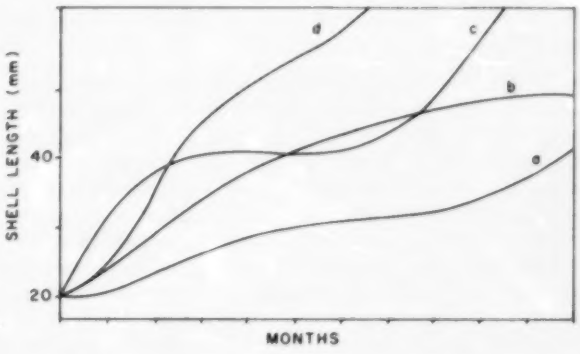


FIG. 3. Growth of suspended *Mytilus edulis* at various localities. a. Anderson Cove, British Columbia, thermal range 5–20°C (Heritage unpublished data). b. Bedford Basin, Nova Scotia, range 0–20°C (Freeman 1974). c. Linne Mhuirich, Scotland range 2.5–20°C (Mason 1969). d. Vigo, Spain range 10–21°C (Andrev 1965).

tion of reserves, and body size. Tissue respiration in poikilotherms is closely related to temperature, but the entire organism may be markedly independent or undergo daily cyclic variations (Mane and Talikhedkar 1976). A further complication is that anaerobic processes are active even in the presence of oxygen (Livingstone 1978; Widdows et al. 1979a) and there exists no simple relationship between ambient oxygen level and anaerobic metabolism. In *M. edulis* at all environmental oxygen partial pressures both aerobic and anaerobic metabolism contribute to the total energy metabolism (Famme et al. 1981). Ventilation is less variable, and as it also represents the equivalent of foraging activity, may provide a better estimate of energy transformation. In the present study both ventilation and oxygen consumption are considered simultaneously, but interpretation is based primarily on ventilation. Oxygen consumption is treated as the overall integrator of metabolic activity.

Ventilation is much in excess of oxygen requirements, even allowing for a low uptake efficiency (Van Dam 1954), and suggestions that it is directly controlled by oxygen demand (Hamwi and Haskin 1969) are probably erroneous (Verduin 1969). Van Winkle (1975) in a review of the relationship was unable to reach an unequivocal conclusion. The fact that *M. edulis* decreases ventilation while increasing oxygen uptake when subjected to reduced environmental oxygen (Bayne 1971b) strongly suggests that ventilation rate in bivalves is not primarily concerned with respiration. Vigorous and protracted ventilation is encouraged by the relative paucity of suspended nutritious particles that may be rapidly depleted in an area densely populated by bivalves (Ryther 1969). Partitioning of assimilated energy between ventilation and other activities is not resolved for bivalves and is complicated by the ventilatory current being both respirational and food-gathering. The theoretical power required to pump a given volume of water is readily calculated from the pallial configuration, water velocity, and Reynold's number, and works out at less than 1% of the total energy budget. However, ventilation is probably a much larger utilizer of energy, as movement of water by cilia is not efficient in large organisms. This view is supported by the correlated drop in oxygen consumption and low levels of ventilation during SMR and its abrupt increase when pumping is resumed. Short-term fluctuations in ventilation are accompanied by large variations in respiration, also demonstrating a direct cause and effect. Attempts to establish the cost of ventilation by summation of the endogenous rate of oxygen consumption of individual tissues was not possible as their respiration is greater than that of the entire organism (Kerkuk and Laverack 1957; Giese 1969). The cost of ventilation and obtaining food by ciliary pumping of water may be a significant size-limiting factor in bivalves; it is significant that the largest bivalves (Tridacnidae) derive a major portion of their nutrition from symbiotic zooxanthellae.

## Size

An extensive literature demonstrates a negative correlation between body size and metabolic rates of invertebrates, including bivalve molluscs (Bayne et al. 1976a; Banse 1979). It is not clear whether this reduction is purely a hydromechanical phenomenon based on an optimum size and configuration of the pallial chamber and ciliated areas, the decreasing proportional gill area, or is due in part to increased diffusion gradients through enlarging tissues (Famme and Kofoed 1980). Age may also have significant influence, resulting in lowered general tissue metabolism (Hopkins 1930) including reduced ciliary activity (Schlieper et al. 1958). Several gerontic *M. edulis* and *P. staminea* had ventilation and oxygen consumption rates substantially less than similar sized, but younger individuals (Fig. 4). Body weight has so marked an effect on metabolism that it is not possible to make a significant comparison between individuals without compensating for size. Further difficulties may be introduced by differential tolerance, as small *M. edulis* are better able to withstand high temperature than large individuals (Bayne et al. 1975). Differences between larval and juvenile stages have not been examined, though larval variations may be present as the respiratory substrate shifts from lipid to carbohydrate (Holland and Hannant 1974).

The effect of size on physiology is complex and probably involves more than a changing requirement based on mechanical constraints or altered demand due to physiological cycle. For instance, small *M. edulis* are more independent of oxygen saturation during hypoxia than large individuals (Famme 1980), when monitored during artificial ventilation. This is opposite to the situation under more normal conditions (Bayne 1971a). Estimates obtained in my study (Table 2) agree with published estimates of oxygen consumption (Bayne et al. 1976a), and most fall within the accepted values of 0.70–0.80 for poikilotherms (Von Bertalanffy 1957). However, very small and negative values are known (Zeuthen 1953; Hughes 1970). The weight exponents for ventilation are generally higher than those calculated for various mytilids (Bayne et al. 1976a), but may reflect the omission of small individuals. The period of thermal acclimation may also significantly affect performance (Kennedy and Mihursky 1972; Dye 1979). The values recorded

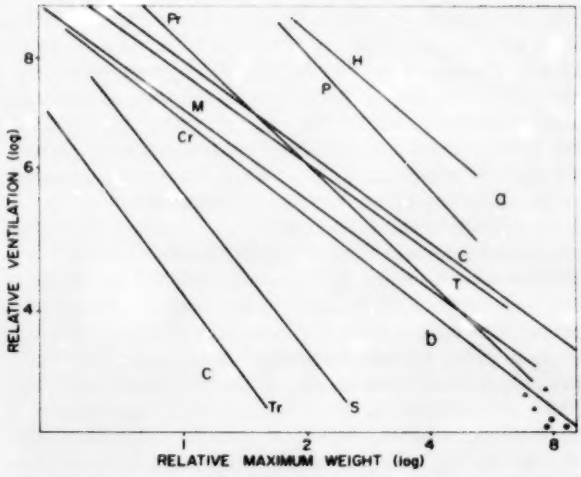


FIG. 4. Ventilation as a function of body size, regressions calculated from observations at 15°C and 29-30‰ salinity. a. High ventilation, rapid decline. b. Medium ventilation, low decline. c. Low ventilation, rapid decline. (C = *C. nuttallii*, Cr = *C. gigas*, H = *H. giganteus*, M = *M. edulis*, P = *P. caurinus*, Pr = *P. staminea*, S = *S. giganteus*, T = *T. philippinarum*, Tr = *T. capax*, ▲ = gerontic *Mytilus edulis*, ● = gerontic *Protothaca staminea*.)

here suggest that both oxygen consumption and ventilation are proportional to body surface area rather than weight.

The weight exponents for oxygen consumption reported here are consistently higher than those for ventilation, also noted by Vahl (1973a, c). The result of this difference is that an increasing portion of the energy budget is required to meet metabolic demands and a decline in growth efficiency (Jorgensen 1976a; Rodhouse 1978). This may be observed in the majority of bivalves, which grow little or not at all after a certain size is attained. Even when gamete production is considered, a large and increasing portion of energy is utilized in activities not leading to somatic or gametogenic production. The chief sink of this energy is probably ventilation, as pumping of water becomes increasingly less efficient the larger the organism.

There is less variation in the estimate of the weight coefficient than the constant, similar to the finding for fish (Paloheimo and Dickie 1966). The significance is not understood, but may be interpreted as the constant varying widely according to both the phenotypic response to environmental conditions and the internal state, which is influenced primarily by the gonadal cycle. The weight exponent, on the other hand, is an index of function closely tied to hydraulics of ventilation. Though the slopes and elevations of the ventilation and oxygen consumption regression lines for the various species are significantly different it is not possible to compare performance of different sized species as a 2 g *M. edulis* is a large mature animal, whereas a similarly sized *T. capax* is juvenile. Use of the standard body weight ($SO_2$, $QV_2$) merely results in an order of function rate. To compare species at approximately the same point in the growth curves, irrespective of size, body weights may be expressed as a percentage of the average maximum weight attained by the population. Similarly, changes of activity levels may be expressed as a percentage of the activity of the smallest individuals recorded. The data so arranged fall into three significantly distinct groups (Fig. 4). The high ventilators, rapidly declining performers, include only the scallops *H. giganteus* and *P. caurinus* (Fig. 4a). This may be due to the open morphology of the pectinid pallium and the large filibranch gill, capable of withstanding little pressure differential. The unfavourable changes in proportional gill area with increasing size (Vahl 1973b) and the lengthening filaments become more susceptible to displacement unless ventilation, and hence the pressure differential, is decreased. A parallel decline but overall lower level of ventilation is shown by the clams *S. giganteus* and *T. capax* (Fig. 4c). The relative low ventilation rates and rapid decline may be due to turbid flow in the enclosed pallial chambers and frictional loss through the long siphons. The scallop was thought to have proportionately higher metabolic rates than sedentary bivalves (Spärck 1936), but later studies showed oxygen consumption of scallops to be similar to those of other bivalves (Van Dam 1954; McLusky 1973). However, swimming may result in a 2.4-fold increase in respiration (MacKay and Shumway 1980). The majority of species examined fall into an intermediate group (Fig. 4b) characterized by relatively high rates of ventilation which gradually decrease with size. These clams are generally smaller than those of group *a* and *c*, and siphons are very short or lacking. It may be speculated that the vertical separation of the three groups is the product of ultimate body size, with the large species showing progressively decreasing ventilation.

The regression lines for oxygen uptake have larger weight coefficients than those for ventilation (Table 1) as they reflect total metabolism, rather than ventilation costs alone. Because ventilation is probably the major utilizer of oxygen, the lines also fall into the grouping given for ventilation (Fig. 4); thus, it may be useful to consider the logarithmic relationship of oxygen consumption to ventilation, or the total oxygen consumption for each 1 L water ventilated (Fig. 5). Analyses of covariance of this relationship demonstrates significant differences, but two general groupings are evident; five species show high oxygen usage in relation to ventilation, which rapidly increases with body weight (Fig. 5a). The scallops, the long siphoned forms, and one short-siphoned species are included in this group. The presence with this group of the scallops may reflect the fact that observations were made at the upper end of their thermal functional range, while *T. capax* and *S. giganteus* may require higher energy expenditures per litre ventilated to overcome frictional losses entailed by the long siphons. The low slope group (Fig. 5b) includes the siphonless or short-siphoned forms, where increasing size does not greatly increase the oxygen used per litre ventilated. The anatomy of *P. staminea* and *T. philippinarum*, particularly siphonal lengths and diameters, is similar, so assignment to high or low ratio groups is not entirely dictated by anatomy. The absolute differences at all body weights irrespective of ultimate size suggest oxygen utilization is a complex expression with genetic components. It may be speculated that the advantages from long siphons, allowing the invasion of the deeply infaunal habitat, are gained at the expense of decreased efficiency of ventilation. The position of the regression lines (Fig. 5) may be considered the expression of "thriftiness" as they reflect the production capacities observed under natural conditions with the species included in group b generally growing faster than those of group a.

## Temperature

The major external factor influencing metabolic rates in poikilotherms is temperature, and its role has been much studied in bivalves (Jorgensen 1966). The behavior of the

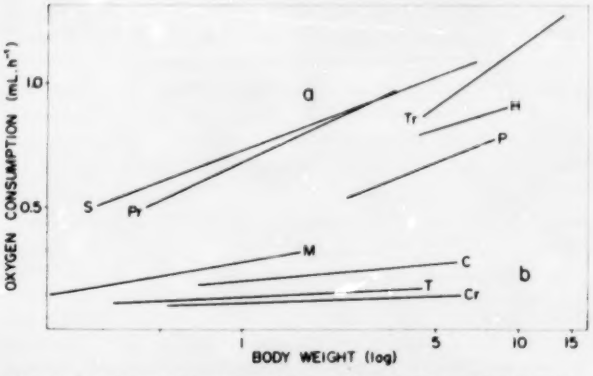


FIG. 5. Total oxygen consumption associated with ventilation of 1 L as function of body weight, regressions calculated from observations at 15°C and 20‰ salinity. a. High oxygen consumption, rapid increase with size. b. Low oxygen consumption, little size effect. Abbreviations as in Fig. 4.

entire organism is a product of the responses of the various tissues, which may differ greatly in their thermal sensitivity (Percy and Aldrich 1971). Thermal tolerance fixes the temperature boundaries in which survival is possible (Gunter 1957). The lower limits have been investigated by Kanwisher (1955) who found that boreal intertidal zone bivalves survive several days exposure at –15°C; however, they succumb after a substantial portion of the tissue water is frozen (Murphy and Pierce 1975). Although a number of widespread seasonal mortalities have been attributed to unusually low winter temperature (Fraser 1921; Blegvad 1929), such severe conditions rarely occur in the region studied. High temperature is a more lethal factor, as many invertebrates succumb to temperatures only slightly above the normal maximum (Kinné 1963) and there exist numerous records of mortalities, particularly of subtidal organisms exposed to warm water (Dickie and Medcof 1963). The stress of high temperature need not manifest itself immediately, as bivalves may withstand excessively high summer temperatures, only to die the following winter (Cronin 1968).

At low temperature there may be no measurable ventilation or oxygen uptake (Thompson and Bayne 1972), equivalent to cold coma (Southward 1958). This lower thermal threshold does not vary significantly in the various species (Fig. 6) and does not appear affected by nutritional state. It is probably a genetically conditioned characteristic, but individual variations are evident. The thermal regimes of the neritic region of the southern portions of the northeastern Pacific are such that the lower thermal threshold does not appear to be a significant factor for survival. The water temperatures are above the threshold at all times, except for intertidal epifauna which may be exposed to much colder air temperatures. There exists no thermal barrier to colonization of deeper waters by the bivalves examined, but only a few species such as *Hiatella arctica* L. have bathymetric ranges from the intertidal zone to 850 m, so it is ecological factors other than the lower thermal threshold that maintain vertical zonational patterns. More commonly, differences in the upper thresholds are small and latitudinal spread is accomplished by bathymetric adjustment, thereby maintaining temperature within the limits of tolerance, as evidenced by the plunging to depth of shallow water northern elements in the southern portions of their range.

The range of temperature over which the organism maintains apparently normal physiological function is the zone of function, though over the long term, activities in suspension-feeders may be grossly imbalanced, and internal functions such as gametogenesis may be suppressed. The size of the zone of function as an index of the ability to tolerate temperature gradients is expected to be larger in intertidal than subtidal organisms, and in those with large latitudinal and bathymetric ranges, than those of more limited distribution.

The upper threshold, although a genetic character, is affected by nutritional state, zonation (Williams 1970), and size, and undergoes seasonal variation as well (Newell and Pye 1970a; Bayne et al. 1977). In species with widespread distribution there may be genetic variability (Prosser 1955) in the environmental extremes tolerated (Vernberg 1962) and the resulting physiological races may be an important preliminary mechanism leading to speciation (Mayr 1963; Jackson 1974). Bivalves as diverse as *Tridacna maxima* and *Mytilus edulis* display high levels of genetic polymorphism of metabolic rates (Ayala et al. 1973; Levington and Koehn 1976) and physiological variability is typical of most groups surveyed. The persistence of these variations may be due to spatial changes of allele frequency with geographic variations of physical regimes (Milkman and Beaty 1970), or due to reversal of latitudinal trends in genotype coincident with a change of allele frequency (O'Gower and Nicol 1968). Physiological performance is the product of interaction of genetic variation and a changing environment that shifts the fitness of a given phenotype. The reactions of the organisms are attempts to achieve equilibrium, so they should be developed in dynamic situations. Physiological heterogeneity is also a system for "spreading the risk" (Reddingius and den Boer 1970) in an unpredictable habitat, so those species with varying sensitivity to environmental factors are, to an extent, preadapted for change. Kauffman (1970, 1972, 1977) found that diverse Cretaceous marine molluscs underwent extinction at high rates during periods of marine regression. Such times would challenge organisms with diminishing niches, high biological competition, and unstable environments due to increased turbidity, decreasing mean temperature and increased seasonality.

The thermal basis for bivalve distribution is difficult to interpret because the majority of temperate boreal shallow water and intertidal species are adapted to short growing seasons, and recruitment is usually irregular. In some years gametes may not be released, while many years planktonic development does not progress to metamorphosis. Bivalve longevity (Comfort 1964) and the relative freedom from predation of adult infaunal species suits them to a life style of sporadic recruitment, temporarily limited somatic growth, and generally low levels of physiological activity.

The bivalves monitored, according to their zones of function (Fig. 6), range from the eurythermic to oligothermic deepwater forms. As expected *M. edulis* and *C. gigas* have the largest zones of function, spanning approximately 24°C. The exact upper boundary, as discussed above, may vary and for *M. edulis* has been given between 27°C (Read and Cumming 1967) and 28.2°C (Wallis 1975), but according to Pearce (1969) byssal attachment and movement are abnormal above 24°C. The cold water cosmopolitan distribution of this species is due primarily to its extreme eurythermicity, but invasion of the tropical zone has been prevented by the upper thermal threshold, and distribution coincides with the 26.7°C isotherm (Wells and Gray 1960). The oyster *C. gigas*

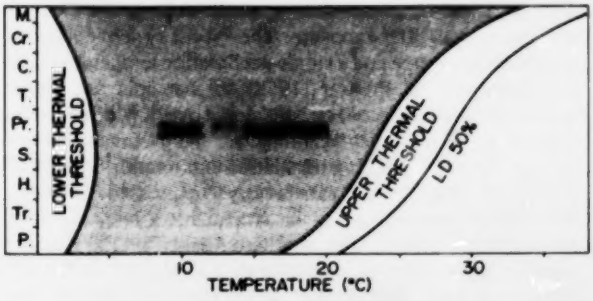


FIG. 6. Thermal tolerances and median mortality (°C) of nine species of bivalves during Routine Metabolic Rate at various temperatures. Salinity 29–30‰. Abbreviations as in Fig. 4.

is equally eurythermic, but favours slightly warmer conditions. Its establishment in cool water regions where post metamorphic individuals flourish is prevented by the high temperatures required for reproduction and metamorphosis (Quayle 1969), while the upper thermal threshold precludes invasion of adjacent tropical areas. The deepwater scallop *P. caurinus* has the narrowest zone of function with erratic behaviour above 16°C. This species is particularly intolerant of unsuitable conditions as these stimulate vigorous shell flapping and swimming reactions, rapidly exhausting the individual.

The limits of the zone of function are fixed genetically, but substantial shifts in thermal optima, mediated by internal factors such as nutrition and gametogenesis, and external factors, especially temperature, result in different ventilation and oxygen consumption rates under identical regimes. Fed individuals respond at RMR which is a function of temperature. A high rate of activity occurs during AMR, but the homeostatic acclimatory mechanism eventually reduces the acute rate. Starvation results in the energy-conserving SMR, characterized by decreased physiological activity and a substantially lower AMR. The scallop *P. caurinus* is the exception, where ventilation and oxygen consumption relationships to temperature are higher during SMR than RMR and no acclimatory mechanism is evident. This organism is adapted to a nearly stable thermal environment, and did not develop a mechanism to reduce effort in response to starvation. In comparison, the closely related, but shallow water *H. giganteus* does display low rates of function during SMR. The R/T relationship of ventilation in the various species may best be compared using $Q_{10}$ indices. The mean 10–20°C $Q_{10}$ during SMR is 3.12 ± 1.09 SD and 1.88 ± 0.27 SD during RMR. The very low and unstable activity levels at the lower end of the zone of function during SMR result in the high $Q_{10}$ and large standard deviations, while acclimation reduces the $Q_{10}$ and makes it more uniform indicating a measure of thermal independence. The decreased rate of activity during SMR is important for suspension feeding bivalves inhabiting temperate and boreal shallow water zones, where high water temperature is usually associated with increased seasonal primary production and abundance of suspended food particles. A decrease in ventilation is necessary to prevent overloading and possible clogging of the pallial apparatus. Conversely, during low temperatures, ventilation must be increased to collect additional scarce food particles. In the region studied, temperature and food abundance may be adequate through much of the year, but somatic growth and gametogenesis of all bivalves occupies only a fraction of the annual cycle, indicating that activity levels are only partially balanced.

Rates of ventilation and oxygen consumption are altered by a change in temperature. The change is initially acute (Kinné 1970), characterized by over-response or "overshoot" and is termed the AMR. This over-reaction may not be apparent in all cold blooded organisms (Grainger 1958; Newell and Northcroft 1967), but is present in the bivalves examined in this study. These transitory levels of activity coincidental with increases of temperature and food supply, may be an efficient mechanism for the exploitation of a fluctuating environment rather than classic stress symptoms. Though the size of the response is dependent on internal physiological state, it is invariably larger for a temperature increase than for a decrease. The AMR elicited by a 5°C rise during SMR results in a mean 10–20°C $Q_{10}$ of 1.74 ± 0.36 SD, while during RMR the $Q_{10}$ is 1.42 ± 0.12 SD. These indices apparently contradict the accepted view that thermal sensitivity of bivalves is reduced during SMR, but in fact the absolute rates of ventilation and oxygen consumption are lower during SMR. This is conveniently expressed by the average *scope for activity*, which for ventilation is 0.87 ± 0.37 during SMR and 1.46 ± 0.38 for RMR. This index is a useful measure of the potential to respond to changing temperature and food supply, and is greater while the bivalve is actively feeding (Fig. 7, 8).

When comparing organisms with different ventilation rates, it is more significant to consider the *ratio of activity*, obtained by dividing rather than substracting as for the scope of activity. This index is usually larger at the lower end of the zone of activity and falls into two major groups. The larger SMR includes bivalves with a higher ratio from SMR, while in the other group the ratio is highest for RMR, and is a function of thermal sensitivity. A further index is the *scope for growth*, representing the energy available for growth and gametogensis after the energy requirements for maintenance and activity metabolism have been met. It is a useful integrative index when stress from various combinations of several physical and chemical factors are monitored. For instance, the scope for growth is reduced in mussels maintained above 20°C (Bayne et al. 1973) and there is a better growth rate of *T. philippinarum* held at 12°C than at higher temperature (Mann and Glomb 1978; Mann 1979). However, it is useful only when effects on a known population are compared and cannot be used to interpret improvement in a previously stressed population.

Acclimation is a homeostatic mechanism maintaining physiological performance commensurate with temperature and food supply, thereby conferring on the organism a degree of thermal independence. Various bivalve tissues have different potential for acclimation (Bass 1977), but in the entire organism it is well developed in those from the littoral zone (Newell 1970) and minimally in those from the subtidal zone (Ansell and Sivadas 1973) that are naturally less subject to large and changeable thermal gradients. The most significant result of thermal acclimation is the shifting of the temperature optimum towards the prevailing value, thereby altering the activity rates in inverse relationship to temperature (Fig. 9).

A scheme for the classification of acclimation was proposed by Precht (1958) and the bivalves examined for the present study fall into Type 3 as acclimation is only partial. The species range from the nearly complete acclimation of *M. edulis* and *C. gigas*, to only slight in *P. caurinus* even after more than 30 d exposure. The Precht system considers only a narrow range and a single acclimation temperature and was improved by Prosser (1958) so that cold and warm acclimated animals could be considered over a wide temperature range. The species examined for the present study belong to Type 4, involving translation and rotation of the R/T curves. Neither system is satisfactory to express the changing acclimatory potential over the annual life cycle, and it is more significant to use the ventilation 10–20°C $Q_{10}$. Excluding *P. caurinus*, the $Q_{10}$ mean for the species is 2.13 ± 0.39 SD during SMR and 1.40 ± 0.13 SD during RMR. The lower value is due to the decreased spread of activity rates between the high and low ends of the zone of function resulting from acclimatory homeostasis.

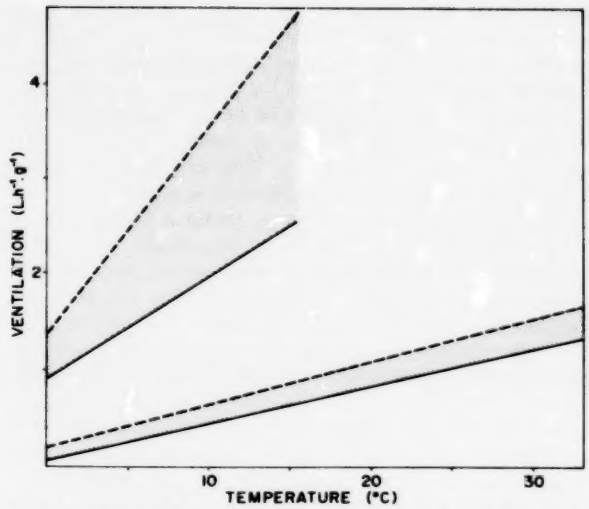


FIG. 7. Calculated regression lines for standard *(solid line)* and acute *(broken line)* ventilation for 5°C increase in temperature for *Mytilus edulis (lower)* and *Patinopecten caurinus (upper)*. Shaded portions represent the scope for activity.

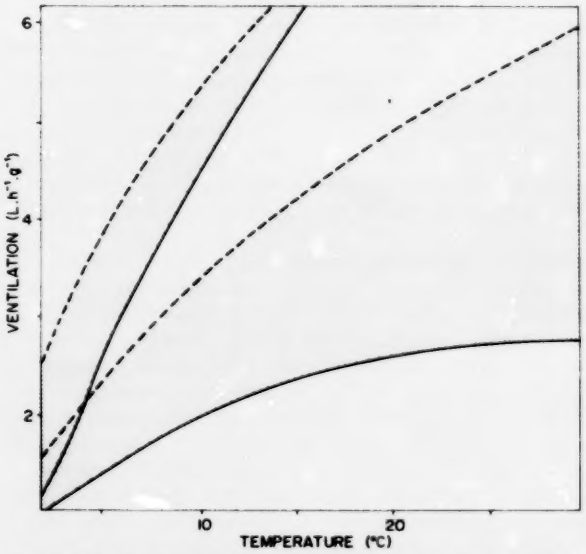


FIG. 8. Calculated regression lines for routine *(solid line)* and acute *(broken line)* ventilation for 5°C increase in temperature for *Mytilus edulis (lower)* and *Patinopecten caurinus (upper)*. Shaded portions represent the scope for activity.

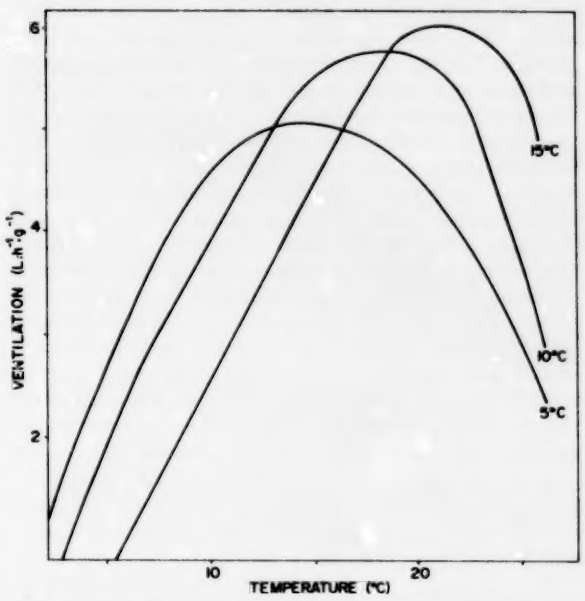


FIG. 9. Relationships between acclimatory temperature and acute ventilation of *Mytilus edulis*.

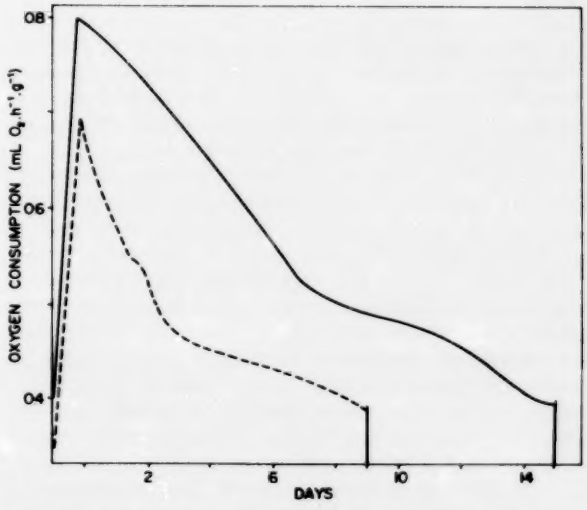


FIG. 10. Oxygen consumption during thermal acclimation of *Crassostrea gigas* after raising temperature from 10–15°C. Intertidal *(broken line)*, subtidal *(solid line)*.

The shift from the transitory acute rate of function immediately after a change of temperature, to the new steady-state after continued exposure, is slow. *M. edulis* requires between 7–30 d (Newell and Pye 1970b; Bayne 1971a; Widdows and Bayne 1971), whereas for the subtidal scallop *Chlamys opercularis* Gmelin requires a minimum of 35 d (McLusky 1973). Acclimation is most complete and rapid in the central part of the zone of function, and towards the thermal extremes it may be only partial or absent (Flügel and Schlieper 1962; Bayne et al. 1977). It functions only within a limited range and abrupt changes greater than 5°C may eliminate or greatly slow the process (Widdows 1973). Individuals located low in the intertidal zone, or those permanently submerged, are subjected to less abrupt thermal fluctuations than those inhabiting high intertidal areas, and may be expected to acclimate more slowly. This is the situation for *C. gigas* taken from the beach compared to those from adjacent rafts at 2-m depths. The initial acute consumption rate of oxygen is lower for the former and the acclimation curve is abrupt (Fig. 10), demonstrating a decreased thermal sensitivity and enhanced homeostatic ability.

Obviously, the time required for acclimation influences ability to colonize regions subject to frequent temperature change. Short term, usually large, thermal fluctuations are withstood by cessation of activity and closure of the shell valves. Longer term conditions result in acclimation, but this need be only partial to maintain an advantageous relationship between energy uptake and expenditure within the zone of function. Acclimation is in fact an entrainment mechanism approximating function to conditions, as demonstrated by Widdows (1976) for *M. edulis*. Compensation to reduced temperature is a different phenomenon from the extensive metabolic adaptions to cold displayed by polar species, which is postulated to be the result of elevated basal metabolism, leading to proportionately less energy for somatic growth and gametogenesis (Dunbar 1968). However, it is more likely due to a net reduction in the overall energy intake (Clarke 1980). The thermal relationships of bivalves are complex and sensitive to numerous external and internal factors, but obvious trends are evident in the different abilities to acclimate, and in the position of the end points of the thermal range, which are reflected in habitat and general distribution both zonal and latitudinal.

## Salinity

Mean salinity is a major factor controlling community distribution, but also important are the effects of its fluctuations. Most marine invertebrates are sensitive to changes in salinity, and its bearing on metabolism has received much attention (Kinné 1964a, b; Remane and Schlieper 1971), particularly for the mussel *M. edulis* where the relationships have been explored in detail (Bayne et al. 1976). No effect due to body size (weight) could be detected in the present study but conflicting reports state that juveniles are more (Fox 1941) or less (Salik 1978) sensitive than adults. This sensitivity to salinity appears to depend on the detection of changes in concentrations of several ions, rather than changes in osmotic pressure (Akberali and Davenport 1982). In *M. edulis* it is mediated by sensors situated on the tentacles of the inhalant siphon (Davenport 1981) but in the infaunal clam *Scrobicularia plana* (daCosta) is more deeply situated (Akberali and Davenport 1982).

Bivalves are apparently incapable of anisosmotic regulation (Schoffeniels and Gilles 1972), but isosomotic interacellular regulators are probably present (Florkin 1962). The initial response to an abrupt change in salinity is closure of the shell valves (Pierce 1971; Gilles 1972), and they may remain tightly closed for days until conditions ameliorate or death occurs. Closure seals out undesirable conditions and avoids necessity to adjust to transitory periods of intolerable salinity. This adaptive behavior may be important, for instance, by allowing *M. edulis* to colonize estuarine zones subjected to fresh water during part of the tidal cycle (Milne 1940). The closure reflex is present in all species examined except the scallop *P. caurinus* which, in the presence of lowered salinity, vigorously flaps its valves, rapidly exhausting itself while exposing the tissues to the inimical conditions.

For salinity changes within the zone of function, intermittent reduced ventilation and oxygen consumption are soon resumed (Lagerspetz and Sirkka 1959), termed the initial "shock" rate by Bayne (1973). The rapidity of response and its interspecific uniformity is possibly attributable to direct interference with the activity of gill cilia (Van Winkle 1972), as observations for entire organisms approximate the values established for isolated bivalve tissues (Vernberg et al. 1963). This is followed by gradual acclimation over a prolonged period (Newkirk et al. 1977; Newkirk 1978). The acclimatory pattern, unlike the initial response, is markedly specific and probably genetically determined, although acclimatory history has an effect. For the nine species examined the process of acclimation is slow and compensation is limited, but except in the case of large salinity alterations (>20‰), sufficient function remains to maintain the organism during acclimation which may occupy several weeks to months. The exception is the scallop *P. caurinus* where no compensatory mechanism is evident. A similar range of sensitivity is also apparent in the oxygen consumption of isolated gill tissue which remains nearly constant between 5–30‰ in *Crassostrea* and *Mytilus*, but is more sensitive in *Mercenaria* and *Modiolus* (Van Winkle 1968). However, salinity tolerances vary with season (Castagna and Chanley 1973), and differences noted in this paper may reflect stages in life-cycle rather than phenotypic variations. The number of days required for partial acclimation of ventilation in each species is represented in Fig. 11.

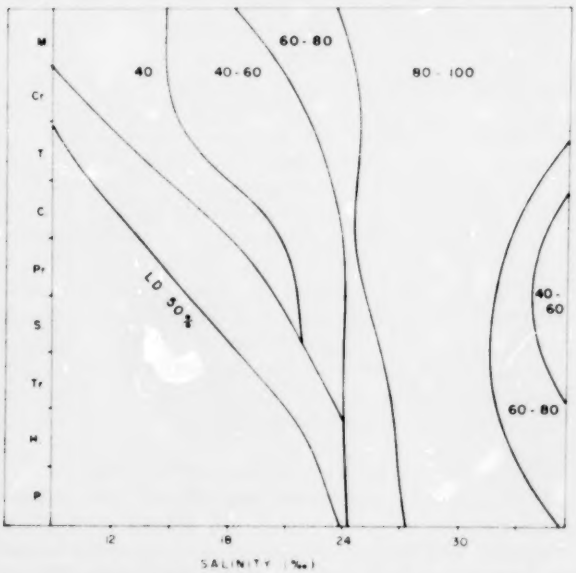


FIG. 11. Summary diagram of percentage recovery of ventilation during acclimation to changes in salinity. Abbreviations as in Fig. 4.

## Oxygen

Environmental oxygen tension has a direct effect on the physiology of bivalves, particularly on heart rhythm (Bayne 1971b; Brand and Roberts 1973), but bivalves in general are rather tolerant of periods of anoxia (Maloeuf 1937; Lent 1968) and have been called euryoxic (Hammen 1976). Too high a saturation may reduce survival of various aquatic

invertebrates (Fox and Taylor 1955). However, except for estuaries and intertidal locations, oxygen levels are not usually limiting in the areas studied, and in anoxic intertidal zones aerial respiration may occur during exposure (Kuenzler 1961; Boyden 1972). The relationship between availability and oxygen uptake in bivalves was examined by Van Winkle and Mangum (1975) who attempted to designate them as regulators or conformers. Many bivalves partially accommodate to reduced oxygen by increasing the efficiency of uptake, usually associated with a reduction in ventilation rate (Van Dam 1954). No bivalves appear to fit entirely into the conformer or regulator category, but response is variable, depending on physiological condition, and may be conforming during starvation (Bayne 1971a) and regulating when fed (Bayne et al. 1976b). Size also appears to have an important effect (Bayne 1971a).

The response of the nine species to lowered oxygen tension involved decreased ventilation and increased efficiency in oxygen uptake. During SMR the $B_2$ coefficient of the quadratic function is low (3.0) compared to the RMR value (8.6), probably indicating higher conformity during SMR. The coefficient $B_2$ may also be a criterion describing interspecific differences of tolerance to reduced oxygen levels. There is a marked negative correlation between $B_1$ and $B_2$ as stated by Van Winkle and Mangum (1975). A regulating organism with respiration independent of ambient concentration would give $B_0 = 0$ and $B_1, B_2 = 0$, while a fully conforming organism would yield $B_0 = 0$, $B_1 = 0$, $B_2 = 0$ (Hammen 1976). The biological significance of the curves summarized in Table 10 is not obvious, except that the regulatory point varies with species. There is no evidence of acclimation to oxygen tension outside the specific tolerance range, though Bayne (1975) stated that *M. edulis* compensates over several days for changes in $PO_2$.

There have been attempts to establish a phylogenetic basis for the response to hypoxia (Hiestand and Stemler 1952), but there exists little evidence that it has biological significance (Prosser and Brown 1961). Simple mechanical constraints probably determine whether oxygen is carried to tissues primarily by direct diffusion, or via circulating body fluids. This results in phylogenetic clustering reflecting common structure (Van Winkle and Mangum 1975). The mean linear and quadratic coefficients of the bivalves studied during SMR and RMR (Table 10) are plotted in Fig. 12 and compared to other taxa. It has been established that nutritional condition has a marked effect on the relationship of $PO_2$ to uptake in an echinoderm (Lane and Lawrence 1979), and there are similar significant differences in the relationships of the nine bivalve species studied. The values for starved individuals (SMR) are more dispersed than the fed (RMR), suggesting that the former reflect the genetically determined condition, while the latter are due to the entraining effect of particle uptake. The calculated values reported here correspond in general with those given for 11 classes of aquatic invertebrates by Van Winkle and Mangum (1975).

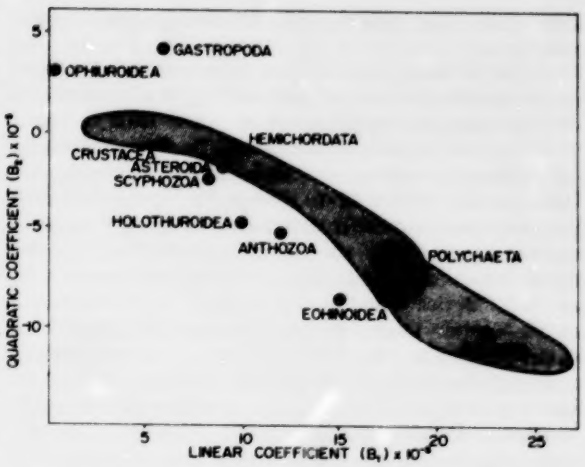


FIG. 12. Mean linear ($B_1$) and quadratic ($B_2$) coefficients of the second degree polynomial regression model of oxygen uptake in relationship to $PO_2$ during SMR *(vertical shading)* and RMR *(horizontal shading)* compared to 11 classes of aquatic invertebrates (from Van Winkle and Mangum 1975).

## Particles

The term "suspension feeder" coined by Hunt (1925) is preferable to "filter feeder" as the latter implies retention of particles too large to pass through a mechanical sieve (Jorgensen 1966). It is known that minute particles may also be efficiently retained, and that the laterofrontal cirri may be the trapping mechanism (Hughes 1975); however, species with short or no cirri are also able to capture minute bodies (Vahl 1973b; Jorgensen 1976b). The structure, physiology, and behaviour of most bivalves have been profoundly modified to exploit suspended particles. A substantial intake is usually necessary, as nutrient content may be low. In Departure Bay, based on dry weight, it varies between 2% (winter) to 23% (summer), so the quantity of particulate material sedimented by bivalves is large. This sedimenting activity of bivalves plays an important transfer role in ecology, by consolidating small suspended particles and making them available to benthic detrivores.

Suspension feeding bivalves are sensitive to change in the quantity and type of particles present in the ventilated stream. Though relationships are unclear and the literature is conflicting, it is likely that suspended material, next to temperature and salinity, is the major external factor influencing ventilation rate and therefore the entire trophic/energetic relationship. Chemosensory and tactile receptors are involved as reactions differ depending on type of particle and there appears to be a significant increase in oxygen uptake efficiency with increasing particle concentration (Widdows et al. 1979b) and there is also a marked sensitivity to dissolved organic substances and algal exudates (Nelson 1960; Ali 1970).

Starved bivalves increase ventilation and oxygen consumption immediately after the addition of food (Thompson and Bayne 1972; Widdows 1973). The higher ventilation is directly linked to increased ciliary action (Bernard unpublished data), but the oxygen consumption rate reflects also the general metabolic acceleration on feeding observed in the majority of poikilotherms. Increased activity is triggered by a *minimum particle* concentration (Thompson and Bayne 1972). For the nine species examined no significant differences could be found in the minimum particle concentration of $0.05 \pm 0.02$ mg·L$^{-1}$ (dry weight) using natural plankton suspensions. This minimum value is ration weight

dependent, rather than based on absolute number of particles.

The literature suggests that at extremely low ration, activity is correlated to food availability until an asymptote is attained when performance remains nearly uniform over a wide range of particle concentration (Thompson and Bayne 1974), though there may be a small decline in ventilatory rate (Hildreth and Mallet 1980). When the heated-thermistor probe was used to monitor ventilation, the species examined did not appear sensitive to particle concentration once the minimum was surpassed. This lower threshold appears to be an on/off device rather than a progressive control mechanism. Contrary evidence is possibly due to the insignificant particle retention immediately following first presentation, termed the lag-phase (Nelson 1960) of the gill not ready to intercept particles. As the ratio of oxygen consumption to ventilation remains constant during the partial retention phase, it is likely that transit through the lag-phase involves purely mechanical adjustments of the gill and cirri.

At concentrations of particles exceeding the minimum, ventilation rates remain nearly uniform over a wide, probably genotypically determined, range. Excessive turbidity suppresses ventilation (Yonge 1926; Davids 1964; Thompson and Bayne 1974) to a point where it becomes erratic and behaviour abnormal, herein termed the *maximum particle concentration*. The value varies with species (Fig. 13) but ranges within the normal annual mean range for surface waters of the Strait of Georgia (Stephens 1966). No clear correlation between body size and ability to handle suspended loads was found, contrary to the evidence that large mussels are more tolerant to turbidity than small mussels (Widdows et al. 1979b). The extremely high maximum turbidity tolerated by the oyster *C. gigas* probably is a factor in its adaptation to estuarine conditions, primarily due to the formation of an ancilliary opening of the suprabranchial chamber (promyal chamber). It is possible that a superabundance of suspended particles may actively improve the performance of the genus *Crassostrea*, as its member species continue to function in water containing very high concentrations of suspended materials.

The proportion of retained particles rejected with the pseudofaeces rapidly increases with turbidity, and the necessary mucus elaborated and lost may result in a net energy debit at very high food concentrations (F. R. Bernard unpublished data). The energy balance is further in favour of low particle concentration when the declining assimilation efficiency as a function of ingested ration is taken into account (Thompson and Bayne 1974). The mere increase of plankton standing stock does not improve the growth rates of bay scallops (Kirby-Smith and Barber 1974). In short, somatic growth of suspension-feeding bivalves does not correlate directly to quantity of available food.

Above the minimum threshold level, number rather than total quantity of suspended particles may influence ventilation rate. The activity levels of some bivalve species are apparently correlated to particle numbers (Winter 1969, 1973). These observations may be partly attributable to the lag-phase, previously mentioned, in adjustment for particle interception, or differential response to particle size or physical characteristics. The basis for the hypothesis of particle selectivity is the common observation that the gut contents usually differ qualitatively from the overlying plankton. Comparisons are invariably made between stomach contents and plankton sampled by net in the water column adjacent to the habitat. Under such conditions wide differences occur, but if the zone close to the substrate is sampled, reflecting the water ventilated, ingested ration conforms to suspended population except for a substantial reduction of the heavier inorganic particles. The concept of the effect of spatial heterogeneity in the quantitative distribution of plankton on the nutrition of suspension feeders was first put forward by Moore et al. (1912). The distinct population of particles available to benthic organisms, termed the hyperbenthos (Beyer 1958), may be the result of hydrological phenomena of flow adjacent to boundaries, or the migration into the water column of benthic materials due to turbulence. It is a neglected aspect of feeding ecology that may radically alter many ideas on the energy relationships of the benthic community.

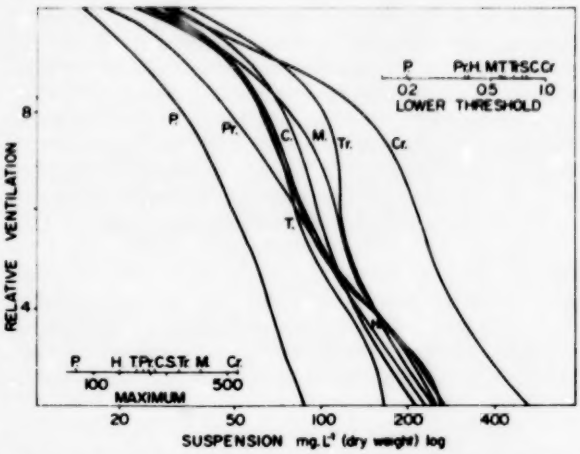


FIG. 13. Effect of suspended particulate material on ventilation of nine species of bivalves. Acclimated at 14°C, 29‰. Inset maximum particle concentration and lower threshold. Abbreviations as in Fig. 4.

A major basis for the sorting hypothesis was the observation (Loosanoff 1949) that the oyster *C. virginica* when presented a mixture of purple sulphur bacteria (*Chromatium* sp.) and a unicellular alga, produced pseudofaeces with a predominance of bacteria and faeces nearly bacteria-free. Bernard (1972) repeated these experiments and concluded that bacteria and alga were equally ingested, but the bacteria were rapidly digested. In all bivalves examined there is no evidence of sorting on the gill or labial palps, but a large proportion of inorganic particles are diverted and rejected with the pseudofaeces (Hughes 1969). Bernard (1974) showed that particles of high specific gravity do not impinge on the gill, but settle on the mantle surface, so bivalve sorting is largely a gravimetric phenomenon. Similar conclusions were reached by Rubenstein and Koehl (1977).

Analysis of particle size distributions before and after passage through the shellfish, using Jacob's Electivity Index (Jacobs 1974) which compares proportion of particles retained to the proportion available in a particular size category, failed to reveal any active selection of particle size after the initial adjustment period. This supports the contention (Möhlenberg and Riisgård 1978) that bivalves do not adjust

retention efficiency in response to environmental factors. However, long-term observation revealed variations possibly reflecting tonus of the gill musculature, though alteration of the velocity of water passing through the gill will also affect the size of particles retained (Rubenstein and Koehl 1977). The shift in particle selectivity of *C. gigas* (Fig. 14) during the annual cycle closely follows that reported for *M. edulis* (Bayne et al. 1977).

No evidence was found of changes in size preference of particles with temperature, and no significant difference could be detected in the particle retention of *C. gigas* and *P. staminea* provided with natural plankton <4 μm diameter as compared to control groups fed unfiltered plankton with a high proportion of particles >15 μm diameter.

While this study revealed no ability to alter particle preference, there were pronounced specific differences in the smallest particle retained (Möhlenberg and Riisgård 1978), and each species showed a substantially different inflexion of the electivity index curve (Fig. 15). These differences may be due to gill morphology, though "open-gilled" (filibranch) types such as *M. edulis* and the scallops retained smallest particles as efficiently as eulamellibranchs. The distance between gill cirri may be important, but species with short or absent cirri efficiently retain small particles. It is probable that individual differences may merely reflect the seasonal cycle demonstrated for *C. gigas* or *M. edulis* and do not indicate resource partitioning among suspension feeders.

The relative retention of the smallest particles is sharply reduced in all species (Fig. 15) as already described in the literature (Haven and Morales-Alamo 1970; Vahl 1973a, b). Estimation of particles <1.5–2.0 μm diameter is impossible because of the production of particles by the clam. This may result in an increase of the population of the smallest particles in the water after passage through the pallium (Vahl 1972; Jorgensen 1975), due either to the separation of larger clumps or suspension of rejecta (Hildreth 1980).

With increasing particle size there is an asymptote after which efficiency does not increase until very large particle diameters are encountered. This probably marks a mechanical limit of the gill morphology, as obviously particles too large to pass between the interfilamental spaces or ostia will be retained. It is obvious that numerous mechanical and physical processes are simultaneously operating during particle retention. The significance of the differential retention of variously sized particles must be interpreted with consideration of the total size spectrum of the available particle populations. Though the smallest particles are poorly retained, their greater abundance may make them a more important food source than the better retained, but more scarce, larger particles.

Discussion of the uptake of natural suspensions by bivalves must also include the effect of associated dissolved substances. It is well established that dissolved inorganic chemicals (Aiello 1960, 1962), as well as organic materials (Collier et al. 1950, 1953) influence metabolism. Oxygen consumption increases in *M. edulis* and *Mya arenaria* with the addition of 200 mg/L glucose (Koller 1930). However, reaction to dissolved proteins, lipids, and carbohydrates appears slight or absent in bivalves (Butler and Wilson 1959) but another study showed that direct assimilation of dissolved organic compounds by the eastern oyster *C. virginica* (Gmelin) may account for up to 16% of net metabolism (Ferguson 1982). These conflicting observations may be due to the presence or absence of particulate material during uptake determinations. When subjects were in SMR in filtered seawater, no effect could be detected on either oxygen uptake or ventilation with glucose up to 250 mg/L. In contrast, during RMR and active feeding, additions of 15 mg/L glucose boosted respiration and ventilation rates. Though there are reports that both the gills (Anderson and Bedford 1973) and the mantle (Steward and Dean 1978) absorb dissolved organics, plugging the mouth prevents substantial uptake of glucose (Yonge 1928; Koller 1930), showing it occurs in the alimentary tract via the feeding mucus, and not through the external epithelia. It may be concluded that for bivalves dissolved organics are not an important energy

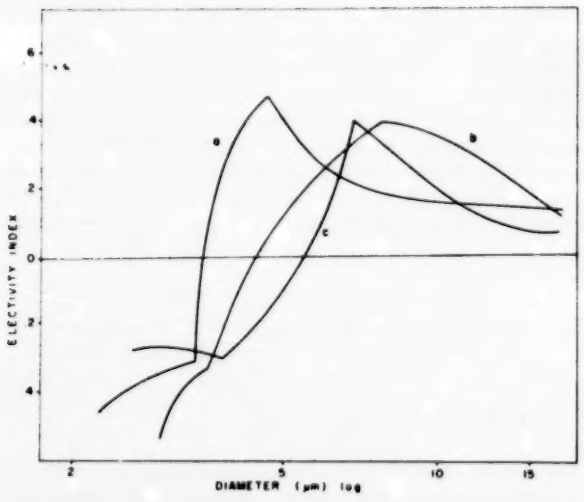


FIG. 14. Electivity of particle retention based on size during March (a), July (b), and November (c) in *Crassostrea gigas*.

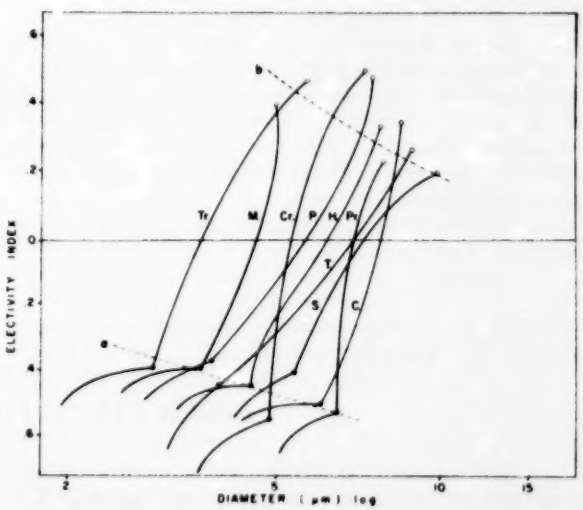


FIG. 15. Electivity of particle retention based on size by nine species of bivalves. a. minimum particle diameter. b. maximum particle selectivity. Abbreviations as in Fig. 4.

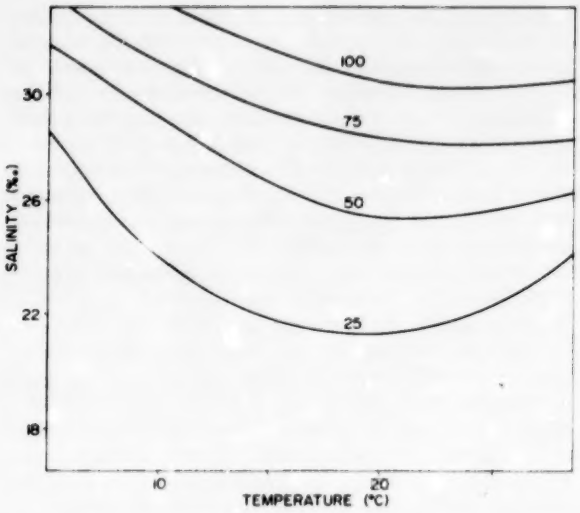


FIG. 16. Response surface calculated for percentage oxygen consumption for *Crassostrea gigas*, as a function of temperature and salinity.

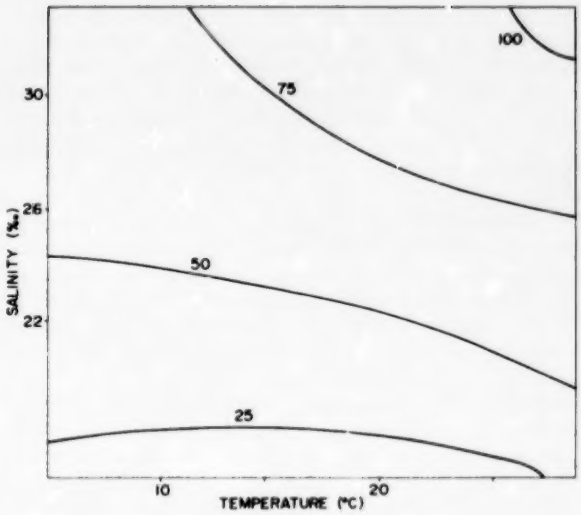


FIG. 17. Response surface calculated for percentage oxygen consumption for *Saxidomus giganteus*, as a function of temperature and salinity.

source and it is probable that the significance of dissolved organics in marine food chains is generally small (Khailov and Finenko 1970).

### Combined effects

An initial step in understanding the physiological responses of an organism is the investigation of the effect of alteration of a single environmental factor, but the implications of a univariable response have little ecological importance. Functional capacity is the sum of numerous, frequently opposing factors acting in concert (Alderdice 1972). Data appearing here and in the literature show that temperature is the dominant determinant of physiological rate of intertidal and neritic zone bivalve molluscs, followed in importance by salinity. Numerous reports deal with their individual effects, but the combined effect of temperature and salinity has been studied only in larval development (Brenko and Calabrese 1969).

At the tissue level of physiological response, it is expected that theoretically lowered salinities result in greater oxygen consumption by marine organisms to satisfy the increased work to maintain osmotic balance. This is the situation reported for one species of shore crab in which oxygen uptake is highest at low salinity and temperature, though a related species displays the opposite pattern (Dehnel 1960). The response of bivalves is more complex, as ventilatory activity is occurring, and this is also sensitive to salinity. As ventilation utilizes the greatest portion of total oxygen uptake, the combined effects of salinity and temperature are influenced by ventilatory responses, rather than simply the metabolic pathways. The relationships are clearly evident when plotted as a response surface graph (Lindsey et al. 1970).

The oyster, *C. gigas* displays a wide toleration range with temperature the dominant factor until the salinity is much reduced (Fig. 16). The infaunal clam, *S. giganteus* has a very narrow range of optimum function limited to high salinity and high temperature (Fig. 17). For this species temperature is dominant only at high salinity. At reduced salinity, the centre of activity changes and salinity assumes the dominant role. The results reported for both species are in direct contrast to those obtained for the shrimp *Crangon crangon* where low salinity is better tolerated at high temperature (Broekema 1941), but agree well with the relationship established for the hydroid *Cordylophora caspia* (Kinné 1956).

## IMPLICATIONS FOR MARICULTURE

I have attempted to identify optimum environmental conditions for bivalves in a way useful to the mariculturist. I have ignored the special requirements of the larvae and concentrated on those stages used for the "grow-out" phases of mariculture. The data and discussion presented above have been treated primarily from the ecological point of view in partial explanation for the distribution of the various species and the compromise necessary for adaptation to different habitats. The same information is also useful for the identification of potential candidates for intensive maricul-

TABLE 11. Optima and ranges of environmental factors for somatic growth in nine species of Bivalvia.

| Species | Temperature °C | | Salinity ‰ | | Suspension mg·L$^{-1}$ | |
|---|---|---|---|---|---|---|
| | Optimum | Range | Optimum | Range | Optimum | Range |
| *Clinocardium nuttallii* | 14 | 10–17 | 28 | 26–31 | 60 | 15–200 |
| *Crassostrea gigas* | 17 | 13–20 | 24 | 16–31 | 120 | 25–550 |
| *Hinnites giganteus* | 13 | 10–16 | 30 | 28–31 | 50 | 10–120 |
| *Mytilus edulis* | 15 | 11–17 | 26 | 18–31 | 90 | 10–400 |
| *Patinopecten caurinus* | 12 | 9–13 | 31 | 28–31 | 35 | 5–95 |
| *Protothaca staminea* | 15 | 12–18 | 27 | 24–31 | 60 | 15–150 |
| *Saxidomus giganteus* | 14 | 10–17 | 26 | 24–31 | 70 | 10–140 |
| *Tapes philippinarum* | 16 | 13–21 | 28 | 24–31 | 55 | 10–135 |
| *Tresus capax* | 13 | 11–18 | 28 | 26–31 | 95 | 15–200 |

ture and the selection of growing sites offering the best chances for success. Knowledge of the physiological responses of a species to environmental conditions may reduce the need for extensive pilot-scale trials and may suggest the reason for unexpected failure and mortalities.

Estimates of optimum and range for salinity and suspended particle concentration, together with similar estimates for temperature promoting active somatic growth, while avoiding gametogenesis (F. R. Bernard unpublished data), are summarized (Table 11). It is significant that the two species having the widest tolerance of environmental conditions, *C. gigas* and *M. edulis*, already support established long-term mariculture industries. Their epithetic habit is probably equally important as it allows ready three-dimensional array in the water column and their byssal attachment or cementation to a substrate permits their convenient manipulation. Doubtless all these factors making the two species amenable to cultivation developed together as adaptations to exploit the variable conditions of the shallow water and intertidal zone.

The infaunal species have a major drawback when considered as mariculture subjects. The lack of some attachment mechanism in the adult makes some form of containment necessary unless a system of semiculture is contemplated where growth after seeding is left to nature. In most cases the lack of extensive suitable foreshore and heavy losses due to predation make this type of operation unprofitable. The clams, *P. staminea*, *S. giganteus*, and *T. philippinarum*, though displaying wide thermal and salinity tolerances, suffer from this disadvantage, and, except for the very shallow burrower *T. philippinarum*, require a compression force on the shell to overcome the opening tension of the ligament. This is usually supplied by the substrate and when absent, death results from exhaustion of the adductor muscles which must be in constant contraction to draw the shell valves together.

The physical optima of the deeply infaunal *T. capax* and the shallow *C. nuttalli* are almost the same, suggesting different strategies for dealing with environmental fluctuations, as the short-siphoned *C. nuttallii* present in the middle- to low-intertidal zone must be subjected to thermal and salinity changes much wider than *T. capax*. *C. nuttalli* is frequently found half-buried and is able to function apparently normally for long periods of time without being buried. *H. giganteus* is not tolerant of reduced salinity, displays a relatively low thermal optimum, and is normally subtidal in distribution, but does occur intertidally where surface waters remain cold. It is the subject of cultivation trials, especially in California, but the relatively slow growth rate in British Columbia and ponderous shell make it unlikely to yield a commercial operation.

The most promising candidate is *P. caurinus* as its epibenthic habit makes it amenable to suspended culture either attached to strings or enclosed in mesh containers. Stimulated by the success in Japan in the cultivation of the closely related *P. yessoensis* (Jay, 1857), trials have begun in British Columbia with *P. caurinus*, but this species appears to be less tolerant than its Japanese relative. It is unlikely that it can be cultivated outside fully marine conditions and then only at sites selected for strong water exchange to avoid plankton blooms or accumulation of inorganic matter of terrestrial origin. The extremely narrow physical environment demanded by *P. caurinus* may account for its comparative rarity and sporadic distribution in British Columbia.

## ACKNOWLEDGMENTS

I am indebted to D. B. Quayle who first interested me in the functional aspects of bivalves and to N. Bourne and other colleagues at the Pacific Biological Station who so kindly read the manuscript and supplied suggestions and criticisms. My thanks are also due to Maureen Palmer for carefully typing the original draft of this paper.

## References


AIELLO, E. L. 1960. Factors affecting ciliary activity on the gill of the mussel, *Mytilus edulis*. Physiol. Zool. 33: 120–135.

1962. Identification of the cilioexcitary substances present in the gill of the mussel *Mytilus edulis*. J. Cell. Comp. Physiol. 60: 17–21.

AKBERALI, H. B., AND J. DAVENPORT. 1982. The detection of salinity changes by the marine bivalve molluscs *Scrobicularia plana* (da Costa) and *Mytilus edulis* L. J. Exp. Mar. Biol. Ecol. 58: 59–71.

ALDERDICE, D. F. 1972. Factor combinations, p. 1659–1722. *In* O. Kinné [ed.] Marine ecology. 1(3) xii + 1245–1774.

ALI, R. M. 1970. The influence of suspension density and temperature on the filtration rate of *Hiatella arctica*. Mar. Biol. 6: 291–302.

ANDERSON, J. W., AND W. B. BEDFORD. 1973. The physiological responses of the estuarine clam, *Rangia cuneata* (Gray), to salinity. II Uptake of Glycine. Biol. Bull. 144: 229–247.

ANDREV, B. 1965. Biologia y parasitologia del mejillon Gallego. Las Ciencias 30: 107–118.

ANSELL, A. D., AND P. SIVADAS. 1973. Some effects of temperature and starvation on the bivalve *Donax vittatus* (da Costa) in experimental laboratory populations. J. Exp. Mar. Biol. Ecol. 13: 229–262.

AYALA, F. J., D. HEDGECOCK, G. S. ZUMWALT, AND J. W. VALENTINE. 1973. Genetic variation in *Tridacna maxima*, an ecological analog of some unsuccessful evolutionary lineages. Evol. 27: 177–191.

BALLENTINE, D. AND J. E. MORTON. 1956. Filtering, feeding, and digestion in the lamellibranch *Lasaea rubra*. J. Mar. Biol. Assoc. U.K. 35: 241–274.

BANSE, K. 1979. On weight dependence of net growth efficiency and pecific respiration rates among field populations of invertebrates. Oecologia 38: 111–126.

BASS, E. L. 1977. Influences of temperature and salinity on oxygen consumption of tissues in the American oyster *(Crassostrea virginica)*. Comp. Biochem. Physiol. 58B: 125–130.

BAYNE, B. L. 1971a. Oxygen consumption by three species of lamellibranch molluscs in declining ambient oxygen tension. Comp. Biochem. Physiol. 40A: 307-313.

1971b. Ventilation, the heart beat and oxygen uptake by *Mytilus edulis* L. in declining oxygen tension. Comp. Biochem. Physiol. 40A: 1065–1085.

1973. The responses of three species of bivalve molluscs to declining oxygen tension and reduced salinity. Comp. Biochem. Physiol. 45A: 793–806.

BAYNE, B. L. 1975. Aspects of physiological condition in *Mytilus edulis* L., with special reference to the effects of oxygen tension and salinity, p. 213-238. *In* H. Barnes [ed.]. Proc. 9th Europ. Biol. Symp. Aberdeen Univ. Press, Aberdeen. 760 p.

1976. [ed.] Marine Mussels: their ecology and physiology. Int. Biol. Programme 10. Cambridge Univ. Press. 506 p.

BAYNE, B. L., R. J. THOMPSON, AND J. WIDDOWS. 1973. Some effects of temperature and food on the rate of oxygen consumption by *Mytilus edulis* L., p. 181–193. *In* W. Wieser, [ed.] Effects of temperature on ectothermic organisms. Springer-Verlag. 298 p.

1976a. Physiology 1, p. 121–206. *In* B. L. Bayne [ed.] Marine mussels: their ecology and physiology. Int. Biol. Prog. 10. Cambridge Univ. Press. 506 p.

BAYNE, B. L., J. WIDDOWS, AND R. I. E. NEWELL. 1977. Physiological measurements on estuarine bivalve molluscs in the field, p. 57–67. *In* B. F. Keegan, P. O. Ceidigh, and P. J. S. Boaden [ed.] Biology of benthic organisms. Proc. 11th Europ. Symp. Mar. Biol. Galway. Pergamon Press. 630 p.

BAYNE, B. L., J. WIDDOWS, AND R. J. THOMPSON. 1976b. Physiological integration, p. 261–291. *In* B. L. Bayne [ed.] Marine Mussels: their ecology and physiology. Int. Biol. Programme 10. Cambridge Univ. Press. 506 p.

BAYNE, B. L., J. WIDDOWS, AND C. WORRALL. 1975. Some temperature relationships in the physiology of two ecologically distinct bivalve populations, p. 379–400. *In* F. J. Vernberg, A. Calabrese, F. P. Thunberg, and W. B. Vernberg [ed.] Physiological responses of marine biota to pollutants. Academic Press. 462 p.

BERNARD, F. R. 1972. Nutrition of *Crassostrea gigas* (Thunberg, 1795): an aspect of estuarine energetics. Ph.D. Thesis. London Univ. 448 p.

1974. Particle sorting and labial palp function in the Pacific oyster *Crassostrea gigas* (Thunberg,1795). Biol. Bull. 146: 1–10.

1983. Physiological responses of bivalve molluscs to environmental changes. Can. Data Rep. Fish. Aquat. Sci. (In press)

BLEGVAD, H. 1929. Mortality among marine animals of the littoral region in ice winters. Rep. Danish Biol. Sta. 35: 49–62.

BOYDEN, C. R. 1972. The behaviour, survival, and respiration of the cockles *Ceratoderma edule* and *C. glaucum* in air. J. Mar. Biol. Assoc. UK 52: 661–680.

BRAND, A. R., AND D. ROBERTS. 1973. The cardiac responses of the scallop *Pecten maximus* L. to respiratory stress. J. Exp. Mar. Biol. Ecol. 13: 29–43.

BRENKO, M. H., AND A. CALABRESE. 1969. The combined effects of salinity and temperature on larvae of the mussel *Mytilus edulis*. Mar. Biol. 4: 224–226.

BROEKEMA, M. M. M. 1941. Seasonal movements and the osmotic behaviour of the shrimp *Crangon crangon* L. Arch. Neerl. Zool. 6: 1–100.

BROWN, F. A. 1954. Persistent activity rhythms in the oyster. Am. J. Physiol. 178: 510–514.

BROWN, F. A., M. F. BENNETT, H. M. WEBB, AND C. L. RALPH. 1956. Persistent daily, monthly and 27-day cycles of activity in the oyster and quahog. J. Exp. Zool. 131: 235–262.

BUTLER, P. A., AND A. J. WILSON. 1959. Relationship of oyster pumping to the carbohydrate concentration of sea water. Conf. Natn. Shellfish Assoc. (1958) 1–3.

CASTAGNA, M., AND P. CHANLEY. 1973. Salinity tolerance limits of some species of pelecypods from Virginia. Malacologia 12: 47–96.

CLARKE, A. 1980. A reappraisal of the concept of metabolic cold adaptation in polar marine invertebrates. Biol. J. Linn. Soc. 14: 77–92.

COLLIER, A., S. M. RAY, AND W. MAGNITZKY. 1950. A preliminary note on naturally occurring organic substances in sea water affecting the feeding of oysters. Science 111: 151–152.

COLLIER, A., S. M. RAY, A. W. MAGNITZKY, AND J. O. BELL. 1953. Effect of dissolved organic substances on oysters. Fish. Bull. U.S. Fish Wildlife Serv. 54: 167–185.

COMFORT, A. 1964. Ageing: the biology of senescence. Holt, Rinehart, and Winston. 3rd ed. 365 p.

CRONIN, L. E. 1968. The impact of thermal releases along the east coast on shellfish. Nat. Resour. Inst. Univ. Maryland Chesapeake Biol. Lab. (68–66) 12 p.

DAVENPORT, J. 1981. The opening responce of mussels *(Mytilus edulis)* exposed to rising sea-water concentrations. J. Mar. Biol. Assoc. 61: 667–678.

DAVIDS, C. 1964. The influence of suspensions of micro-organisms of different concentrations on the pumping and retention of food by the mussel (*Mytilus edulis* L.) Netherlands J. Sea. Res. 2: 233–249.

DE WILDE, P. A. W. J. 1973. A continuous flow apparatus for long-term recording of oxygen uptake in burrowing invertebrates; with some remarks on the uptake in *Macoma bathica*. Netherlands J. Sea Res. 6: 157–162.

DEHNEL, P. A. 1960. Effect of temperature and salinity on the oxygen consumption of two intertidal crabs. Biol. Bull. 118: 215–249.

DICKIE, L. M., AND J. C. MEDCOF. 1963. Causes of mass mortalities of scallops *(Placopecten magellanicus)* in the southwestern Gulf of St. Lawrence. J. Fish. Res. Board Can. 20: 451–482.

DUNBAR, M. J. 1968. Ecological development in polar regions. Prentice Hall. 119 p.

DYE, A. H. 1979. The effect of acute and long term temperature changes on the respiration of two sand-dwelling bivalves. Comp. Biochem. Physiol. 63A: 405–409.

ENRIGHT, J. T. 1965. The search for rhythmicity in biological time-series. J. Theor. Biol. 8: 426–468.

FAMME, P. 1980. Oxygen-dependence of the respiration by the mussel *Mytilus edulis* L. as a function of size. Comp. Biochem. Physiol. 67A: 171–174.

FAMME, P., AND L. H. KOFOED. 1980. The ventilatory current and ctenidial function related to oxygen uptake in the declining oxygen tension by the mussel *Mytilus edulis* L. Comp. Biochem. Physiol. 66A: 161–171.

FAMME, P. J. KNUDSEN, AND E. S. HANSEN. 1981. The effect of oxygen on the aerobic-anaerobic metabolism of the marine bivalve, *Mytilus edulis* L. Mar. Biol. Lett. 2: 345–351.

FERGUSON, J. C. 1982. A comparative study of the net metabolic benefits derived from the uptake and release of free amino acids by invertebrates. Biol. Bull. 162: 1–17.

FLORKIN, M. 1962. La regulation isosmotique intracellulaire chez les invertebres marins euryhaline. Bull. Acad. Roy. Belgique. Sci. 48: 687–694.

FLÜGEL, H., AND C. SCHLIEPER. 1962. Der Einfluss physikalischer und chemischer Faktoren auf die cilienaktivitat und Pumparte der Miesmuschel *Mytilus edulis* L. Kiel. Meeresforsch. 18: 51–66.

FOX, D. L. 1941. Changes in the tissue chloride of the California mussel in response to heterosmotic environments. Biol. Bull. 80: 111–129.

FOX, H. M., AND A. E. R. TAYLOR. 1955. The tolerance of oxygen by aquatic invertebrates. Proc. Roy. Soc. London 143B: 214–225.

FRASER, C. MCLEAN. 1921. Some apparent effects of severe weather on the n rine organisms in the vicinity of Departure Bay, B.C. Contr. Can. Biol. 1918–1920: 29–33.

FREEMAN, K. R. 1974. Growth, mortality, and seasonal cycle of *Mytilus edulis* in two Nova Scotia embayments. Fish. Mar. Ser. Tech. Rep. 500: 112 p.

FRY, F. E. J. 1947. Effects of the environment on animal activity. Univ. Toronto Stud. Biol. 55: 1–62.

GIESE, A. C. 1969. A new approach to the biochemical composition of the mollusc body. Oceanogr. Mar. Biol. Rev. 7: 175–229.

GRAINGER, J. N. R. 1958. First stages in the adaptation of poikilotherms to temperature change, p. 79–91. *In* C. L. Prosser [ed.] Physiological adaptation. Am. Physiol. Soc. 185 p.

GUNTER, G. 1957. Temperature, p. 159–184. *In* J. W. Hegepeth [ed.] Treatise on marine ecology and paleoecology. Geol. Soc. Am. Mem. 67. 1127 p.

HALCROW, K., AND C. M. BOYD. 1967. The oxygen consumption and swimming activity of the amphipod *Gammarus oceanicus* at different temperatues. Comp. Biochem Physiol. 23A: 233–242.

HALEY, L. E., G. F. NEWKIRK, D. W. WAUGH, AND R. W. DOYLE. 1975. A report on the quantitative genetics of growth and survivorship of the American oyster, *Crassostrea virginica* under laboratory conditions. 10th Europ. Symp. Mar. Biol. Belgium 1: 221–228.

HAMMEN, C. S. 1976. Respiratory adaptations: Invertebrates, p. 347–355. *In* M. Wiley [ed.] Estuarine Processes 1. Academic Press. 541 p.

HAMWI, A., AND H. H. HASLIN. 1969. Oxygen consumption and pumping rates in the hard clam *Merceneria mercenaria*: the direct method. Science 163: 823–824.

HAVEN, D. S., AND R. MORALES-ALAMO. 1970. Filtration of particles from suspension by the American oyster *Crassostrea virginica*. Biol. Bull. 139: 2498–264.

HIESTAND, W. A., AND F. W. STEMLER. 1952. Acquired tolerance of insects to anoxia. Physiol. Comp. Oecol. 2: 362–370.

HILDRETH, D. I. 1980. Bioseston production by *Mytilus edulis* and its effect in experimental systems. Mar. Biol. 55: 309–315.

HILDRETH, D. I., AND D. J. CRISP. 1976. A corrected formula for calculation of filtration rate of bivalve molluscs in an experimental flowing system. J. Mar. Biol. Assoc. UK 56: 111–120.

HILDRETH, D. I., AND A. MALLET. 1980. The effect of suspension density on the retention of 5 m diatoms by the *Mytilus edulis* gill. Biol. Bull. 158: 316–323.

HOLLAND, D. L., AND P. J. HANNANT. 1974. Biochemical changes during growth of the spat of the oyster, *Ostrea edulis* L. J. Mar. Biol. Assoc. UK 54: 1004–1016.

HOPKINS, H. S. 1930. Age differences and the respiration of muscle tissue of mollusks. J. Exp. Zool. 56: 209–240.

HUGHES, R. N. 1969. A study of feeding in *Scrobicularia plana*. J. Mar. Biol. Assoc. U.K. 49: 802–823.

1970. An energy budget for a tidal-flat population of the bivalve *Scrobicularia plana* (Da Costa). J. Anim. Ecol. 39: 357–381.

HUGHES, T. G. 1975. The sorting of food particles by *Abra* sp. (Bivalvia: Tellinacea). J. Exp. Mar. Biol. Ecol. 20: 137–156.

HUNT, O. D. 1925. The food of the bottom fauna of the Plymouth fishing grounds. J. Mar. Biol. Assoc. UK 13: 560–599.

IVLEV, V. S. 1961. Experimental ecology and the feeding of fishes. Yale Univ. Press. 302 p.

JACKSON, J. B. C. 1974. Biogeographic consequences of eurytopy and stenotopy among marine bivalves and their evolutionary significance. Am. Nat. 108: 541–560.

JACOBS, J. 1974. Quantitative measurement of food selection. Oecologia 14: 413–417.

JORGENSEN, C. B. 1966. Biology of suspension feeding. Int. Monogr. Pure & Applied Sci. Pergamon Press 27: 357 p.

1975. Comparative physiology of suspension feeding. Ann. Rev. Physiol. 37: 57–79.

1976a. Growth efficiencies and factors controlling size in some mytilid bivalves, especially *Mytilus edulis* L.: review and interpretation. Ophelia 15: 175–192.

1976b. Comparative studies on the function of gills in suspension feeding bivalves, with special reference to effects of serotonin. Biol. Bull. 151: 331–343.

KANWISHER, J. W. 1955. Freezing in intertidal animals. Biol. Bull. 109: 56–63.

KAUFFMAN, E. G. 1970. Population systematics, radiometrics, and zonation — a new biostratigraphy. Proc. N. Am. Paleont. Conf. (F): 612–666.

1972. Evolutionary rates and patterns of North American Mollusca. Internat. Geol. Congr. 24th (Sec. 7): 174–189.

1977. Evolutionary rates and biostratigraphy, p. 109–141. *In* E. G. Kauffman and J. E. Hazel [ed.] Concepts and methods of biostratigraphy. Dowden, Hutchinson and Ross. 658 p.

KENNEDY, V. S., AND J. A. MIHURSKY. 1972. Effect of temperature on the respiratory metabolism of three Chesapeake Bay bivalves. Chesapeake Sci. 13: 1–22.

KERKUK, G. A., AND M. S. LAVERACK. 1957. The respiration of *Helix pomatia*: a balance sheet. J. Exp. Biol. 34: 97–105.

KHAILOV, K. M., AND Z. Z. FINENKO. 1970. Organic macromolecular compounds dissolved in sea-water and their inclusion in food chains, p. 16–18. *In* J. H. Steele [ed.] Marine food chains. Univ. Calif. Press. 552 p.

KINNÉ, O. 1956. Über den Einfluss des Salzgehaltes und der Temperatur auf Wachstum, Form und Vermehrung bei ben Hydroidpolypen *Cordylophora caspia* (Pallas), Thecata, Clavidae. 1. Mitteilung uber der Einfluss des Salzgehaltes auf Wachstum und Entwicklung mariner, brackischer, und limnischer Organismen. Zool. Jahrb. Abt. Allg. Zool. Physiol. 66: 565–638.

1963. The effects of temperature and salinity on marine and brackish water animals 1. Temperature. Oceanogr. Mar. Biol. Ann. Rev. 1A: 301–340.

1964a. Non-genetic adaptation to temperature and salinity. Helgolander Wiss. Meeresunters. 9: 433–458.

1964b. The effects of temperature and salinity on marine and brackish water animals. Oceanogr. Mar. Biol. Ann. Rev. 2: 281–339.

1970. Temperature — invertebrates, p. 407–514. *In* O. Kinné [ed.] Marine ecology. Wiley-Intersciences 1: 917 p.

KIRBY-SMITH, W. W., AND R. T. BARBER. 1974. Suspension-feeding aquaculture systems: effects of phytoplankton concentration and temperature on growth of the bay scallop. Aquaculture 3: 135–145.

KLEIBER, M. 1961. The fire of life: an introduction to animal energetics. Wiley. 454 p.

KOLLER, C. 1930. Versuche an marinen Wirbellosen uber die Aufnahme geloster Nahrstoffe. Z. Vgl. Physiol. 11: 437–447.

KUENZLER, E. J. 1961. Structure and energy flow of a mussel population in a Georgia salt marsh. Limnol. Oceanogr. 6: 191–204.

LAGERSPETZ, K., AND A. SIRKKA. 1959. Versucheuber den Sauerstoffverbranch von *Mytilus edulis* aus dem Brackwasser der finnishen Kuste. Kiel. Meeresforsch. 15: 89–96.

LANE, J. M., AND J. M. LAWRENCE. 1979. The effect of size, temperature, oxygen level and nutritional condition on oxygen uptake in the sand dollar, *Mellita quinqueperforata* (Leske). Biol. Bull. 157: 275–287.

LENT, C. M. 1968. Air gaping by the ribbed mussel, *Modiolus demissus* (Dillwyn). Effects and adaptive significance. Biol. Bull. 134: 60–73.

LEVINGTON, J. S., AND R. K. KOEHN. 1976. Population genetics of mussels, p. 357–384. *In* B. L. Bayne [ed.] Marine Mussels: their ecology and physiology. Int. Biol. Programme 10 Cambridge Univ. Press. 506 p.

LINDSEY, J. R., D. F. ALDERDICE, AND L. V. PIENAAR. 1970. Analysis of non-linear models — the non-linear response surface. J. Fish. Res. Board Can. 27: 765–791.

LIVINGSTONE, D. R. 1978. Anaerobic metabolism in the posterior adductor muscle of the common mussel *Mytilus edulis* L. in responce to altered oxygen tension and temperature. Physiol. Zool. 51: 131–139.

LOOSANOFF, V. L. 1949. On the food selectivity of oysters. Science 110: 122.

LOOSANOFF, V. L., AND C. A. NOMEJKO. 1946. Feeding of oysters in relation to tidal stages and to periods of light and darkness. Biol. Bull. 90: 244–264.

MACKAY, J., AND S. E. SHUMWAY. 1980. Factors affecting oxygen consumption of the scallop *Chlamys delicatula* (Hutton). Ophelia 19: 19–26.

MALOEUF, N. S. K. 1937. Studies on the respiration (and osmoregulation) of animals. 1. Animals without an oxygen transporter in the internal medium. Z. Vgi. Physiol. 25: 1–28.

MANE, W. H., AND P. M. TALIKHEDKAR. 1976. Respiration of the wedge clam *Donax cuneatus*. Indian J. Sci. 5: 243–246.

MANN, R. 1979. The effect of temperature on growth, physiology, and gametogenesis in the Manila clam *Tapes philippinarum* (Adams and Reeve, 1850). J. Exp. Mar. Biol. Ecol. 38: 121–133.

MANN, R., AND S. J. GLOMB. 1978. The effect of temperature on growth and ammonia excretion of the Manila clam *Tapes japonica*. Mar. Sci. 6: 335–339.

MASON, J. 1969. Mussel raft trials succeed in Scotland. World Fishing 18: 22–24.

MAYR, E. 1963. Animal species and evolution. Harvard Univ. Press. 767 p.

MCCAMMON, H. M. 1965. Filtering currents in brachipods measured with a thermistor flowmeter. Trans. Ocean. Sci. Eng. 2: 772–779.

MCLUSKY, D. S. 1973. The effect of temperature on the oxygen consumption and filtration rate of *Chlamys (Aequipecten) opercularis* (L) (Bivalvia). Ophelia 10: 141–154.

MILKMAN, R., AND L. D. BEATY. 1970. Large-scale electrophoretic studies of allelic variation in *Mytilus edulis*. Biol. Bull. 139: 430 p.

MILNE, A. 1940. Some ecological aspects of the intertidal area of the estuary of the Aberdeenshire Dee. Trans. R. Soc. Edin. 60: 107–139.

MÖHLENBERG, F., AND H. V. RIISGÅRD. 1978. Efficiency of particle retention in 13 species of suspension feeding bivalves. Ophelia 17: 239–246.

1979. Filtration rate, using a new indirect technique, in 13 species of suspension feeding bivalves. Mar. Biol. 54: 143–147.

MORTON, B. 1970. The tidal rhythm and rhythm of feeding and digestion in *Cardium edula*. J. Mar. Biol. Assoc. U.K. 50: 488–512.

MURPHY, D. J., AND S. K. PIERCE. 1975. The physiological basis for changes in the freezing of intertidal molluscs. 1. Response to subfreezing temperatures and the influence of salinity and temperature acclimation. J. Exp. Zool. 193: 313–322.

NELSON, T. C. 1960. The feeding mechanism of the oyster. II On the gills and palps of *Ostrea edulis*, *Crassostrea virginica*, and *C. angulata*. J. Morphol. 107: 163–191.

NEWELL, R. C. 1966. The effect of temperature on the metabolism of poikilotherms. Nature 212: 426–428.

1970. Biology of intertidal animals. Logos Press, London. 555 p.

NEWELL, R. C., AND H. R. NORTHCROFT. 1967. A re-interpretation of the effect of temperature on the metabolism of certain marine invertebrates. J. Zool. 151: 277–298.

NEWELL, R. C., AND V. I. PYE. 1970a. Seasonal changes in the effect of temperature on the oxygen consumption of the winkle *Littorina littorea* (l) and the mussel *Mytilus edulis* L. Comp. Biochem. Physiol. 34A: 367–383.

1970b. The influence of thermal acclimation on the relation between oxygen consumption and temperature in *Littorina littorea* (L) and *Mytilus edulis* L. Comp. Biochem. Physiol. 344A: 385–397.

NERKIRK, G. 1978. Interaction of genotype and salinity in larvae of the oyster *Crassostrea virginica*. Mar. Biol. 48: 227–234.

NEWKIRK, G., D. L. WAUGH, AND L. E. HALY. 1977. Genetics of larval tolerance to reduced salinities in two populations of oysters, *Crassostrea virginica*. J. Fish. Res. Board Can. 34: 384–387.

O'GOWER, A. K., AND P. I. NICOL. 1968. A latitudinal cline of haemoglobins in a bivalve mollusc. Heredity 23: 485–492.

PALOHEIMO, J. E., AND L. M. DICKIE. 1966. Food and growth of fishes. II. Effects of food and temperature on the relation between metabolism and body weight. J. Fish. Res. Board Can. 23: 869–908.

PAPARO, A. 1973. Innervation of the gill epithelium of the bivalve *Elliptio complanata*. Comp. Gen. Pharmacol. 4: 117–126.

PEARCE, J. B. 1969. Thermal addition and the benthos, Cape Cod Canal. Chesapeake Sci. 10: 227–233.

PERCY, J. A., AND F. A. ALDRICH. 1971. Metabolic rate independent of temperature in mollusc tissue. Nature 231: 393–394.

PIERCE, R. J., R. L. WILEY, AND T. E. WISSIG. 1973. Interconversion of units in studies of the respiration of aquatic organisms. Prog-Fish. Cult. 35: 207–208.

Pierce, S. K. 1971. Volume regulation and valve movements by marine mussels. Comp. Biochem. Physiol. 39A: 103–117.

Precht, H. 1958. Concepts of the temperature adaptations of unchanging reaction systems of cold-blooded animals, p. 50–78. *In* C. L. Prosser [ed.] Physiological adaptation. Ronald Press Co. 185 p.

Prosser, C. L. 1955. Physiological variation in animals. Biol. Rev. 30: 229–262.

1958. The nature of physiological adaptation, p. 167–180. *In* C. L. Prosser [ed.] Physiological adaptation. Ronald Press Co. 185 p.

Prosser, C. L., and F. A. Brown. 1961. Comparative animal physiology. Sanders Co. 688 p.

Quayle, D. B. 1964. Distribution of introduced marine Mollusca in British Columbia. J. Fish. Res. Board Can. 21: 1155–1181.

1969. Pacific oyster culture in British Columbia. Bull. Fish. Res. Board Can. 169: 193 p.

Read, K. R. H., and K. B. Cumming. 1967. Thermal tolerance of the bivalve molluscs *Modiolus modiolus* L., *Mytilus edulis* L., and *Brachidontes demissus* Dillwyn. Comp. Biochem. Physiol. 22A: 149–155.

Reddingius, J., and P. J. Den Boer. 1970. Simulation experiments illustrating stabilization of animal numbers by spreading risk. Oecologia 5: 240–284.

Remane, A., and C. Schlieper. 1971. Biology of brackish water. Wiley-Interscience. 372 p.

Riisgård, H. V. 1977. On measurements of the filtration rates of suspension feeding bivalves in a flow system. Ophelia 16: 167–173.

Roddhouse, P. G. 1978. Energy transformation by the oyster *Ostrea edulis* L. in a temperate estuary. J. Exp. Mar. Biol. Ecol. 34: 1–22.

Rubenstein, D. I., and M. A. R. Koehl. 1977. The mechanisms of filter feeding: some theoretical considerations. Am. Nat. 111: 981–994.

Rytiher, J. H. 1969. The potential of the estuary for shellfish production. Proc. Nat. Shellfish Assoc. 59: 18–22.

Salik, K. Y. M. 1978. Salinity tolerance of *Meretrix casta* (Chemnitz). Bull. Dep. Mar. Sci. Univ. Cochin. 9: 96–104.

Schlieper, C., and R. Kowalski. 1956. Uber den Einfluss des Mediums auf die thermische und osmotische Resistenz des Keimengewebes der Micsmuschel *Mytilus edulis* L. Kiel. Meeresforsch. 12: 37–45.

Schlieper, C., R. Kowalski, and P. Erman. 1958. Beitrag zur okologischzellphysiologischen Charakterisierung des boealen Lamellibranchier *Modiolus modiolus* L. Kiel. Meeresforsch. 14: 3–10.

Schoffeniels, E., and R. Gilles. 1972. Ionoregulatin and osmoregulation in Mollusca, p. 393–420. *In* M. Florkin and B. T. Scheer [ed.] Chemical zoology. Mollusca. Academic Press. 7: 567 p.

Sheldon, R. W., and T. R. Parsons. 1967. On some applications of the Coulter Counter to marine research. Fish. Res. Board Can. MS Rep. 214: 36 p.

Southward, A. J. 1958. Note on the temperature tolerance of some intertidal animals in relation to environmental temperatures and geographical distribution. J. Mar. Biol. Assoc. UK 37: 49–66.

Spärck, R. 1936. On the relation between metabolism and temperature in some marine lamellibranchs and its ecological and zoogeographical importance. Biol. Medd. 13: 1–27.

Stephens, K. 1966. Seasonal changes in the vertical distribution of particulate and soluble material in Departure Bay, B.C. Fish. Res. Board Can. MS Rep. 904: 32 p.

Steward, M. G., and R. C. Dean. 1978. Amino acid absorption and assimilation in the shipworm *Bankia gouldi*. Am. Zool. 18: 575.

Strickland, J. D. H., and T. R. Parsons. 1968. A practical handbook of seawater analysis. Bull. Fish. Res. Board Can. 167: 311 p.

Thompson, R. J., and B. L. Bayne. 1972. Active metabolism associated with feeding in the mussel *Mytilus edulis* L. J. Exp. Mar. Biol. Ecol. 9: 111–124.

1974. Some relationships between growth, metabolism, and food in the mussel, *Mytilus edulis* L. Mar. Biol. 27: 317–326.

Vahl, O. 1972. Efficiency of particle retention in *Mytilus edulis* L. Ophelia 10: 17–25.

1973a. Porosity of the gill, oxygen consumption and pumping rate in *Cardium edule* (L) (Bivalvia). Ophelia 10: 109–118.

Vahl, O. 1973b. Efficiency of particle retention in *Chlamys islandica* (O. F. Muller). Astarte 6: 21–25.

1973c. Pumping and oxygen consumption rates of *Mytilus edulis* of different sizes. Ophelia 12: 45–52.

Van Dam, L. 1954. On the respiration of scallops (Lamellibranchia). Biol. Bull. 107: 192–202.

Van Winkle, W. 1968. The effects of season, temperature and salinity on the oxygen consumption of bivalve gill tissue. Comp. Biochem. Physiol. 26A: 69–80.

1972. Ciliary activity and oxygen consumption of excised bivalve gill tissue. Comp. Biochem. Physiol. 42A: 473–485.

1975. Problems in establishing the relationship between pumping rate and oxygen consumption rate in the hard clam, *Mercenaria mercenaria*. Comp. Biochem. Physiol. 50A: 657–660.

Van Winkle, W., and C. Mangum. 1975. Oxyconformers and oxyregulators: a quantitative index. J. Exp. Mar. Biol. Ecol. 17: 103–110.

Verduin, J. 1969. Hard Clam pumping rates: energy requirements. Science 166: 1309–1310.

Vernberg, F. J. 1962. Comparative physiology: latitudinal effects on physiological properties of animals. Ann. Rev. Physiol. 25: 517–546.

Vernberg, F. J., C. Schlieper, and D. E. Schneider. 1963. The influence of temperature and salinity on ciliary activity of excised gill tissue of molluscs from Northern Carolina. Comp. Biochem. Physiol. 4A: 271–285.

Wallis, R. L. 1975. Thermal tolerance of *Mytilus edulis* of eastern Australia. Mar. Biol. 30: 183–191.

Wells, H. W., and I. E. Gray. 1960. The seasonal occurrence of *Mytilus edulis* on the Carolina coast as a result of transport around Cape Hatteras. Biol. Bull. 119: 550–559.

Widdows, J. 1973. Effect of temperature and food on the heart beat, ventilation rate, and oxygen uptake of *Mytilus edulis*. Mar. Biol. 20: 269–276.

1976. Physiological adaptation of *Mytilus edulis* L. to cyclic temperatures. J. Comp. Physiol. 105: 115–128.

Widdows, J., and B. L. Bayne. 1971. Temperature acclimation of *Mytilus edulis* with reference to its energy budget. J. Mar. Biol. Assoc. UK 51: 827–843.

Widdows, J., B. L. Bayne, D. R. Livingstone, R. I. E. Newell, and P. Donkin. 1979a. Physiological and biochemical responses of bivalve molluscs to exposure to air. Comp. Biochem. Physiol. 62A: 301–308.

Widdows, J., P. Fieth, and C. M. Worrall. 1979b. Relationships between seston, available food and feeding activity in the common mussel *Mytilus edulis*. Mar. Biol. 50: 195–207.

Wieser, W. 1973. Temperature relations of ectotherms: a speculative review, p. 1–23. *In* W. Wieser [ed] Effects of temperature on ectothermic organisms. Springer-Verlag. 562 p.

Williams, R. J. 1970. Freezing tolerance in *Mytilus edulis*. Comp. Biochem. Physiol. 35A: 145–161.

Winter, J. E. 1969. Über den Einfluss des Nahrungskonzentration und andered Faktoren auf Filtierleistung un Nahrungsausnutzung der Muscheln *Arctica islandica* und *Modiolus modiolus*. Mar. Biol. 4: 7–135.

1973. The filtration rate of *Mytilus edulis* and its dependence on algal concentration, measured by a continuous automatic recording apparatus. Mar. Biol. 22: 317–328.

YONGE, C. M. 1926. Structure and physiology of the organs of feeding and digestion in *Ostrea edulis*. J. Mar. Biol. Assoc. UK 14: 295–386.

1928. The absorption of glucose by *Ostrea edulis*. J. Mar. Biol. Assoc. UK 15: 643–653.

ZEUTHEN, E. 1953. Oxygen uptake as related to body size in organisms. Quart. Rev. Biol. 28: 1–12.